The effects of low summer discharge on salmonid ecosystems.

By Jessica Picken

Statement of Originality

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Chapter 5 – David Maxwell statistician at Cefas aided in data preparation and statistics guidance.

Thesis abstract

The chalk streams of England are predominantly groundwater fed and, as a consequence, have a high base flow index. Increasing water demand and resulting abstraction from the groundwater aquifers that support chalk stream flows, coupled with reduced recharge of aquifers as a consequence of projected climate change, are among the biggest threats to the condition of chalk stream ecosystems. Despite this, the ecological implications of the potential changes in river discharge have received limited attention, at a river level. This PhD research used a large(stream)-scale discharge manipulation experiment in three chalk streams within the River Itchen catchment (Hampshire, UK), where sluice gates at the top of each stream enabled complete control of discharge, to investigate the ecosystem level response to simulated drought (reduced summer discharge). Experimental summer discharge reductions of 50% and 90% were selected based on long-term records of summer discharge (1975 – 2018) on the River Itchen and River Test, and implemented on each of the three streams over three consecutive years using a temporal block design. Physical characteristics, basal resources and macroinvertebrates in the streams were monitored, as well as the diet, habitat use, growth, movement and population size of the salmonids present. Sampling occurred before, during and after a 30-day long reduction in discharge each summer. Changes in the physical habitat were quantified by repeated recordings of water depth, velocity, wetted width and temperature, and samples of basal resources (FPOM, CPOM, benthic algae) were taken. The response of macroinvertebrates and prey availability for salmonids was determined by collecting Surber and drift net samples. Salmonid diet was quantified by analysing stomach contents and salmonid movements were monitored using Passive Integrated Transponder (PIT) tag technology. Salmonid populations were monitored using electrofishing. Despite substantial reductions in water depth, velocity and wetted width, and an increase in mean and variation of water temperature, there were limited changes in basal resources and no effect on macroinvertebrate density as a result of

discharge reduction. Reduced discharge resulted in a significant change in macroinvertebrate community composition, but the size of the effect was small in comparison with the variation between sampling occasions (seasonal response). In addition to a limited response by invertebrates, salmonids displayed high dietary plasticity. For example, 0+ trout consumed larger prey items within the discharge reduction treatments compared with the control. Site loyalty decreased for salmon, 0+ and ≥2+ trout during the 90% discharge reduction. Older (≥2+) trout were more likely to move out of the affected area during a 90% discharge reduction, which corresponded with reduced site loyalty. Salmon were the only species/cohort to move back into the study area after the reinstatement of pre-manipulation discharge, potentially due to reduced competition by older (≥2+) trout. There were no lasting effects of discharge reduction on site loyalty, which indicates that these salmonids were resilient to reduced discharge conditions. Yearling (1+) trout adopted a 'sit it out' strategy during reduced discharge conditions. Adopting this strategy increased growth rate and allowed for the expansion of area used once discharge was reinstated to pre-manipulation levels. There were no effects of discharge reduction on population size, although there was a slight (but not significant) effect on salmonid population density after the streams had experienced a 90% discharge reduction. In addition, differences amongst streams could not explain any additional variation within the salmonid data. This research highlights that, despite a marked response in the recorded physical characteristics of the streams, macroinvertebrates and salmonids within these chalk streams display a remarkable resistance/resilience to short term summer discharge reduction. This suggests that they are highly adaptable species and during short-term summer discharge reduction it may be better for river managers to not intervene, even under severe discharge reductions.

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First and foremost, I would like to thank my supervisors John Iwan Jones, Rasmus Lauridsen, William “Bill” Riley and Pavel Kratina for their support throughout this journey. With three summers worth of fieldwork forming the backbone of this project it wouldn’t have been possible without the help and support of all involved whether in the field or at the lab so I offer a huge thank you to: QMUL river communities group (John Murphy, James Pretty, Amanda Arnold and Chas Duerdoth), GWCT fisheries team (Bill Beaumont, Luke Scott, Stephen Gregory and Jess Marsh), Cefas salmon and freshwater team (Mark Ives, Phil Davison, David Maxwell and Luke Aislabie), Winchester collage river keeper Mark Sankey for use of the study site and Environment Agency (Southern Region) staff, in particular Richard Redsull, Heb Leman and Dave Hunter. Finally, a big thank you to my parents and Harry for believing in me from the start and providing the constant supply of sustenance during the final writing months.

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Chapter 1: General introduction

1.1 Chalk stream ecosystems

Most of the worlds chalk streams (c. 85%) occur within southern and eastern England, making them a unique and quintessential part of the landscape (O'Neil & Hughes, 2014). Their distribution mirrors that of the underlaying calcareous chalk, that stretches from Dorset to Norfolk with additional locations in Yorkshire, Lincolnshire and the North and South Downs (see Figure 1.1).

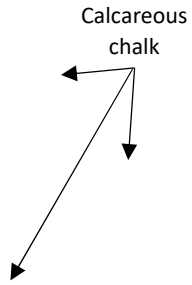

Figure 1.1: Geological map of Britain highlighting the distribution of calcareous chalk. Edited from: www.bgs.ac.uk. Accessed: 19/04/2019

Chalk is a very porous form of limestone and when it rains, water percolates down through the rock to form aquifers: when the aquifer overflows and meets the surface, chalk streams arise (Berrie, 1992). Due to this, chalk streams exhibit certain characteristics. These characteristics include: 1) a high base flow index (this index is a measure of the ratio of long-term baseflow to total stream flow), usually greater than 0.9 (Marsh & Hannaford, 2008), 2) a relatively consistent temperature regime due to the stabilising influence of groundwater discharge (Mackey & Berrie, 1991; Caissie,

2006), 3) an abundant growth of aquatic macrophytes, which is characteristic of many lowland rivers (Franklin *et al*., 2008) and 4) the filtering effects of the chalk before the water enters the river create clear alkaline waters (O'Neill & Hughes, 2014). Typically, clear waters are maintained for the length of the stream due to chalk streams having low turbulent velocities (Sear *et al*., 1999).

The combination of these characteristics helps sustain high levels of biodiversity and macroinvertebrate density (Wright & Symes, 1999). Of UK's chalk streams, 15% are designated Sites of Special Scientific Interest (SSSI), with some areas receiving additional protection and designated Special Areas of Conservation (SACs) under the European Habitat Directive for sustaining wildlife of international importance, e.g. water crowfoot (*Ranunculus penicillatus* (Dumort.) Bab.), southern damselfly (*Coenagrion mercuriale* (Charpentier, 1840)), white clawed crayfish (*Austropotamobius pallipes* (Lereboullet, 1858)) and Atlantic salmon (*Salmo salar* Linnaeus, 1758), hereafter salmon (Environment Agency, 2004; O'Neill & Hughes, 2014). It has been suggested that the importance of England's 224 chalk streams is analogous to biodiversity hot spots such as the Great Barrier Reef and tropical rainforests (O'Neil & Hughes, 2014). However, despite their ecological importance, the Environment Agency and WWF-UK recently concluded that English chalk streams are in a shocking state of health (Environment Agency, 2004; O'Neill & Hughes, 2014).

1.2 Climate change and human impact on the river discharge regime of chalk streams

A natural river flow regime, defined as the range and variation of natural and unaltered flows (Poff *et al*., 1997), is fundamental in order to help maintain a healthy river (Davies *et al*., 2014; Poff *et al*., 2018). It is often considered to be the driving variable for a multitude of instream processes, which in turn affect the organisms living within them (Bunn & Arthington, 2002; Acreman *et al.*, 2008). As chalk stream discharges have a high groundwater component, imbalances in the aquifer (e.g. net loss of water stored within the aquifer) that feed them could result in reduced discharge levels (Westwood *et al*., 2017). Reduced discharge can negatively impact the riverine ecosystem (Rolls *et al*., 2012; Hauer *et al*., 2013). Specifically, projected climatic change coupled with increasing water demands in the chalk region amounts to the biggest threat to chalk stream ecosystems.

Climate change is a major threat globally, with dominant greenhouse gasses such as: carbon dioxide, methane and nitrous oxide being released into the atmosphere at alarming rates (Blunden & Arndt, 2016). The greenhouse effect is a natural process that warms the earth's surface (Mitchell, 1989). However, increased human activity, specifically burning fossil fuels, agriculture and land clearance, are raising the concentrations of greenhouse gasses in the atmosphere, known as the enhanced greenhouse effect, which is contributing to accelerated warming of the earth's atmosphere (Hook & Tang, 2003). Globally, the last 5 years (2014 – 2018, inclusive) have been the warmest years on record with the temperature anomalies ranging from .75 to .95 °C (NOAA, 2019a), with 2019 following the same trend (NOAA, 2019b).

Specifically, the climate change projections for the UK, as laid out by the UK Climate Projections 2009 (UKCP09), predict a shift in UK weather where Southern UK will experience wetter winters but hotter drier summers (Murphy *et al*., 2009). Although wetter winters will increase groundwater recharge potential (Jackson *et al*., 2011), drier summers will lower groundwater levels (Herrera-Pantoja & Hiscock, 2008), resulting in reduced stream discharge and higher air temperatures that will increase evaporation and sensible heat transfer, thus impacting stream temperatures (Webb & Zhang, 1999; Hannah & Garner, 2015).

Drier hotter summers will increase the demand for water from human activities (Van Loon *et al*., 2016). The biggest demand for water during summer months is from agriculture and the potential change in the summer climate will further increase water demand particularly if supplementary irrigation from rivers is needed (Evans, 2017). Along with arable farming, livestock will be affected also: Wall *et al*. (2010) observed reduced milk yields and increased cow mortality as the result of heat stress on dairy cow production over some UK regions, which will further put strain on water demands if bathing stations are required. In addition, compared with the rest of the UK, Southern UK has seen a disproportionate rise in population growth, with the population increasing by 3.8 % – 6.2 % from mid-2013 to mid-2018, a trend which is set to continue over, and likely beyond, the next couple of decades (Coates *et al*., 2019). Chalk aquifers provide 70% of the public drinking water in south-east England

(Visser *et al*., 2019), hence population growth will put further pressure on water resources (Richter *et al*., 2003; Arthington *et al*., 2018).

The pressures which chalk streams face, raises significant concerns regarding the freshwater organisms inhabiting them and their resistance (the ability to withstand) and resilience (the ability to return to a reference state after the disturbance) to changing discharge conditions (Pimm, 1984; Ledger *et al*., 2012; Visser *et al*., 2019).

1.3 Effects of reduced stream discharge on salmonid ecosystems

Natural variations in river discharge influence the spatial and temporal distribution of aquatic biota including fish (Jowett *et al*., 2005; Poff and Zimmerman, 2010). Human perturbation of discharge, either by directly extracting water and regulating rivers or indirectly via changes in land use, can cause disruptions to the aquatic community (Freeman *et al*., 2001; Park *et al*., 2006; Benejam *et al*., 2010). Habitat loss is the most fundamental impact of discharge reduction (Bond *et al*., 2008; White *et al*., 2016; Chadd *et al*., 2017; Rolls & Bond, 2017). Critical stages of habitat loss are: 1) loss of established margins reduce lateral connectivity due to a break in surface water connections between the stream and its riparian zone (Lake, 2003), 2) loss of shallow sections such as riffles reduce longitudinal connectivity such that only isolated pools remain (Boulton, 2003), and 3) in very severe drought, surface flow can be lost completely resulting in the elimination of above ground aquatic life (Boulton, 2003; Lake 2003). Stream type and the severity of discharge reduction will ultimately determine the extent of habitat loss (Lake, 2003).

Changes in habitat availability and associated abiotic variables caused by reduced discharge will have knock-on effects, either immediately or over time, on the riverine ecosystem (Figure 1.2 and Table 1.1). For example, reduced discharge could have immediate effects on salmonid density as fish are concentrated in a smaller stream area as a result of reduced wetted width (Teichert *et al*., 2010). However, over time, a reduction in prey availability may alter salmonid diet and reduce growth rates, as resources become limited (Ward *et al*., 2009), which could result in weaker/less fit fish being lost from the population, thus reducing density. Therefore, the duration and

intensity of discharge reduction are important factors to consider and can produce variable effects. One would expect higher resilience and resistance of aquatic biota to natural low flow events, or artificial low flow events within the natural range of variation, to which fish have adapted over time (Lytle & Poff, 2004), compared with ones which occur outside of the current natural discharge regime.

Overall the general consensus within the literature is that discharge reduction alters and negatively impacts salmonid ecosystems due to a reduction in habitat quantity and quality (Dudgeon *et al*., 2006; Jonsson & Jonsson, 2009; Warren *et al*., 2015; Walters *et al*., 2016). However, the effects of discharge reduction may not be distributed evenly throughout the catchment. Within chalk streams it is likely that, due to a changing climate and increased groundwater abstraction, small streams of naturally shallower depths and narrower wetted widths higher up in the catchment will be impacted the most (Riley *et al.,* 2018). These small streams are important nursery habitats for salmonids (Riley *et al*., 2009a) and can contain high densities of juveniles compared with the main-stream channel (Armstrong *et al*., 2003). Due to the complexity of salmonid ecosystems, and freshwater ecosystems as a whole, their protection is perhaps the ultimate conservation challenge (Dudgeon *et al*., 2006).

The majority of studies that have explored the effects of discharge reduction on freshwater ecosystems only investigate certain aspects. For example, Dewson *et al*., (2007a) investigated how physical changes, as a result of discharge reduction, influenced basal resources in small streams, but little attention was given to other influences on basal resources such as macroinvertebrates. In addition, only extreme levels of discharge reduction were investigated (ranging from -86.2% to -95%). Studies that investigated a broader range of discharges tend to lack physical site details. Westwood *et al*. (2017) investigated variations in discharge on chalk stream macrophyte and macroinvertebrate assemblages at 76 different sites (on 10 ephemeral rivers) but, as flow permanence was the only variable included within the analysis, the mechanisms for the impact of reduced discharge was unknown.

In order to try and better understand how discharge reduction may affect aquatic communities, artificial channel (mesocosm) experiments have been used, as tight control over experimental conditions can provide a mechanistic understanding to

ecosystem responses under extreme events and replication potential is high (Ledger *et al*., 2013; Boersma *et al*., 2014). In one of the few studies to include fish, Teichert *et al*. (2010) investigated how reduced discharge altered salmon habitat, density and growth rate within mesocosms. Although a comprehensive investigation was undertaken where an array of abiotic variables were recorded (depth, velocity, wetted width, sediment and temperature), the physical constraints of the experimental mesocosms (100 m x 1.5 m) could compromise potential responses and interactions among different components of the ecosystem. It is known that the scale at which investigations are undertaken influences the results, tending to overemphasise effects that manifest at small spatial and temporal scales (Bresford & Jones, 2010). In addition, other mesocosm experiments have focussed in the response of invertebrates, but typically used drought treatments that do not represent projected future changes in the UK climate e.g. drought conditions lasting 17 months (Aspin *et al*., 2019a).

At the stream-scale, some have taken advantage of the natural layout of small streams and have been able to manipulate their discharge. Nuhfer *et al*. (2017) reduced stream discharge by excavating a diversion channel and Riley *et al*. (2009a) lowered the sluice gates at the top of the stream. In both cases there was no control treatment (no change in discharge) and no replication of the treatments. Control treatment are important to enable the influence of reduced discharge on the aquatic community to be compared against the natural variation in communities over time, which enables a better attribution of how reduced discharge influences aquatic communities. In addition, the lack of replication reduces the reliability of any interpretation of the data, making it harder to attribute any differences in the data to the treatments.

As it stands there are no stream-scale studies which take a bottom-up ecosystem approach to understand how discharge reduction influences aquatic communities. Bottom up approaches facilitate a good understanding of changes between abiotic variables (the bottom levels), this information can then be used to explain why certain biotic variable responses manifest. Aquatic community response to discharge reduction maybe immediate or develop overtime, but only when a suite of

abiotic variables and biotic variables are monitored can true pathways of causality be identified. Using current literature, a summary of salmonid ecosystem response to the effects of reduced discharge has been represented diagrammatically (Figure 1.2), where hypotheses represent each pathway (Table 1.1).

Replicated bottom-up stream-scale experiments that are of sufficient scale to allow both interactions among different ecosystem components and natural behavioural responses to changing conditions need to take place. The treatments used in such experiments should be representative of future climate projections, and control treatments should be integrated into the experimental design. Only then can a thorough investigation be achieved, which encompasses both the effects of discharge reduction on the riverine community and helps disentangle why certain effects occur.

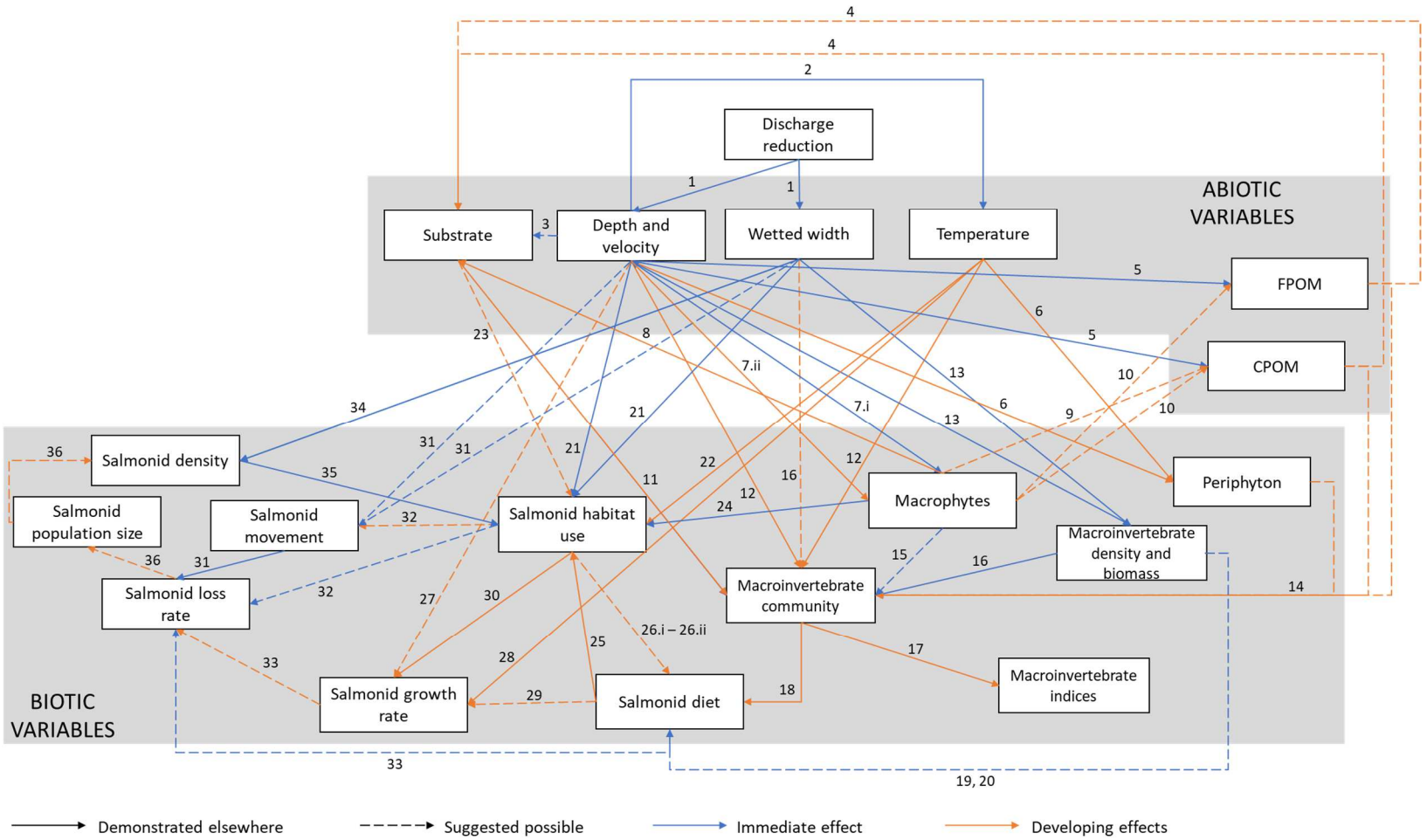

Figure 1.2: Summary of how reduced discharge may affect the salmonid ecosystem in chalk streams. Demonstrated elsewhere = studies that provide proof to a link; Suggested possible = studies suggest an indirect/weak influence on the link; Immediate effects = ones which are impacted directly by reduced discharge; Developing effects = effects which may manifest over time.

Table 1.1: Hypotheses and reference associated with link numbers within Figure 1.2.

Variable	Link number	Hypotheses	Reference
Physical characteristics	1	Discharge reduction will result in a decrease in stream depth, velocity and wetted width	Acreman & Dunbar (2010); Dewson *et al*. (2007b); House *et al*. (2017)
	2	Decrease in stream depth and velocity will a) cause mean temperature to increase and b) the variation in temperature to increase as sensible heat transfer is enhanced	Webb & Zhang (1999); Warfe *et al*. (2014)
	3	Reduced stream velocity will increase deposited fine sediment though settlement	Jones *et al*. (2014)
	4	Increased settlement of FPOM and CPOM (and inorganic matter) will block interstices and access to hyporheic zone	Bo *et al*. (2007); Vadher *et al*. (2015)
Basal resources	5	Reduced stream velocity will increase FPOM and CPOM through settlement due to lower carrying capacity of the water	Walters & Post (2011)
	6	Increases in stream temperature and reduced depth will increase periphyton via warmer shallower waters allowing more light penetration	Lake (2003); Suren *et al*. (2003); Zhao *et al*. (2018)
Macrophytes	7.i	Reduced stream depth and velocity will result in the macrophytes taking up a larger percentage of the aquatic habitat, this will a) cause velocity of the water to decrease further and b) buffer the water depth reduction with discharge due to increased water resistance	Green (2006); Bal & Meire (2009); Rovira *et al*. (2016)
	7.ii	Macrophyte growth will decline due to reduced space (depth & width), and reduced stream velocity causing increased competition for CO_2 and higher O_2 concentrations (during daylight) as low flows reduce replenishment of water	Franklin *et al*. (2008); Spoljar *et al*. (2017)
	8	Reduced discharge will increase fine sediment within macrophyte stands as they will further slowdown water velocity, so particles fall out of suspension	Sand-Jensen, (1998); Luhar *et al*. (2008); Rovira *et al*. (2016)
	9	Increased sedimentation within macrophyte stands (see 8) may a) reduce macrophyte growth if sediments settle on photosynthetic parts and b) cause plant break up resulting in increased levels of CPOM	Jones *et al*. (2012)

	10	Discharge reduction will result in an increase in FPOM and CPOM via entrapment in macrophytes	Raikow *et al*. (1995); Jones *et al*. (2012)
Macroinvertebrates	11	Changes in the dominant substrate type, such as increased proportion of fine sediment patches (see 3), will cause substantial change to the macroinvertebrate community due to changing habitat	Bo *et al*. (2007); Larsen *et al*. (2011); Extence *et al*. (2013)
	12	Shifts in habitat availability due to decreased stream depth/velocity and increased temperature fluctuations will alter the macroinvertebrate community through removal of sensitive taxa and increases in taxa more tolerant of altered conditions	Westwood *et al*. (2017): Aspin *et al*., (2009b)
	13	Reduced stream wetted width will temporarily increase macroinvertebrate density and biomass through reduced habitat space (change will be proportional to loss of habitat [wetted width])	Wright & Berrie, (1987); Acuña *et al*. (2005); Dewson *et al*. (2007b)
	14	Potential increases in basal resources will influence the macroinvertebrate community due to changes in food availability	Kominoski *et al*. (2009); Ledger *et al*. (2013); Alberts *et al*. (2018)
	15	Persistence of macrophytes during reduced discharge will help maintain the macroinvertebrate community by providing food and shelter	Walker *et al*. (2013); Westwood *et al*. (2017)
	16	Increased density of macroinvertebrates (as a result of reduced wetted width) will alter macroinvertebrate community via competition for refugia and predation between taxa but also via movement of more mobile taxa	Wood & Armitage (2004); James *et al*. (2008a); Lake (2011); Lancaster & Ledger (2015)
	17	Changes in the macroinvertebrate community could alter biotic indexes through removal of sensitive taxa and increases in taxa more tolerant of altered conditions	Monk *et al*. (2006); Dunbar *et al*. (2010)
Salmonid diet	18	Changes in the macroinvertebrate community will alter the prey available for fish	Elliott (1973); White & Gowan (2014); Ryan & Kelly-Quinn (2015)
	19	Increased macroinvertebrate density will increase the numbers of drifting macroinvertebrates, which is a primary feeding strategy for salmonids, leading	James *et al*. (2008b); Lake (2011); Weber *et al*. (2014)

		to increased consumption rates.	
	20	Reduced macroinvertebrate biomass will reduce food availability for fish leading to reduced consumption rates	Ledger *et al*. (2011); Dodrill *et al*. (2016)
Salmonid habitat use	21	Reduced stream depth/velocity and wetted width will have direct effects on salmonid habitat use through reduced availability of suitable habitat	Riley *et al*. (2009a)
	22	Increase in temperature variation may influence salmonid habitat use if fish avoid thermally challenging patches	Baird & Krueger, (2003); Dugdale *et al*. (2016)
	23	Change in available substrate might influence salmonid habitat use based on preferred feeding substrate	Kemp *et al*. (2011)
	24	Change in macrophytes will affect fish habitat use via shelter and potential food source	Riley *et al*. (2006); Riley *et al*. (2009a&b); House *et al*. (2017)
	25	Reduced food availability for salmonid diet will increase fish territory size	Gunnarsson & Steingrímsson (2011)
	26.i	Fish will change habitat use to maintain consumption rate and/or to maintain a refuge from potential predators	Armstrong *et al*. (2003); Orpwood *et al*. (2006)
	26.ii	Changes in habitat use may influence prey consumed by fish (gut contents)	Nislow *et al*. (1998); Descroix *et al*. (2009); Giller & Greenberg (2015)
Salmonid growth	27	Decreased stream water depth and velocity may affect fish growth rate as energy required to hold a position in the stream may be less	Fausch, (1984); Harvey *et al*. (2006); VerWey e*t al*. (2018)
	28	Temperature changes will affect fish growth rate via metabolic rate	Higley *et al*. (1986); Neuheimer & Taggart (2007) ; Jones *et al*. (2013)
	29	Change in salmonid diet might affect growth rates due to alterations in prey availability and abundances	Ward *et al*. (2009)
	30	Changes in fish habitat use will affect growth rates if fish have to expend more energy foraging	Girard *et al*. (2004); Lindeman *et al*. (2015)

Salmonid movement	31	Reduction in available habitat will cause salmonid habitat use to change and salmonids will move out of the affected area due to increased population density and competition	Greenberg (1994); Armstrong *et al*. (1998); Davey *et al*. (2006)
Salmonid loss	32	Change in salmonid habitat use, as a result of reduced discharge, may increase the loss of individuals from the population due to a) increased visual clarity for avian predators, b) increased piscivory by larger fish as density is higher under reduced discharge and c) lack of cover/refuge as river margins are lost	Steinmetz *et al*. (2003); Jensen *et al*. (2004); Harris *et al*. (2008); Riley *et al*. (2009a);
	33	Reduced salmonid growth rate will lead to increased loss of individuals from the population via mortality, with less fit individuals being more susceptible to predation and starvation	Biro *et al*. (2006); Hyvärinen & Huusko (2006)
Salmonid population	34	Salmonid population density (ind m^{-2} river) will increase due to reduced width of the stream (change will be proportional to loss of habitat [wetted width])	Stradmeyer *et al*. (2008); Teichert *et al*. (2010)
	35	Increased population density, under reduced discharge conditions, will alter fish territory size due to increased competition for resources	Lindeman *et al*. (2015)
	36	Increased salmonid loss via movement out of the stream area and predation will reduce population size and density	Elliott (1994); Milner *et al*. (2003); Einum *et al*. (2006)

1.4 Water resource management

In England, household water demands have been increasing since the 1950s (Defra, 2011). Since 1970s water abstraction licencing on chalk streams has been authorised whilst also trying to protect the aquatic ecosystem (Giles *et al*., 1988). In 1989, the water industry was privatised, since then over £90 billion has been invested to improve licence management, water infrastructure and raise environmental standards (Defra, 2011).

Despite the Environment Agency regulating abstraction licencing (Environment Agency, 2019), ecological standards set out by the Water Framework Directive (WFD) in 2000 are still not being met (WWF, 2014). Roughly 80% of chalk streams are currently classified as having poor ecological status (WWF, 2014). In 2013, the Department for Environment Food & Rural Affairs (Defra) released a consultation report outlining plans to reform the water abstraction management system, with an overall aim of promoting resilient economic growth whilst protecting the aquatic environment (Defra, 2013). In the hope of protecting future river and aquifer levels, Defra implemented a water management plan that has a strong catchment focus (Defra, 2017a). Although efforts have been made, nationally and locally, to reduce abstraction (WWF, 2009; HM Government, 2011; Southern Water, 2014), in 2017 Defra announced that current water management is not efficient and minimum environmental standards are still not being met (Defra, 2017b).

Salmonids are of great economic and ecological importance to the UK (Armstrong *et al*., 1998; Winfield, 2016), and, in addition to water management strategies promoting the maintenance of acceptable stream discharges, a wealth of rapid fire assessments and more complex hydro-ecological models have attempted to predict the response of fish populations to changes in river discharge (Maddock, 1999). Physical Habitat Simulation System (PHABSIM; Milhous *et al*., 1989) is one of the most frequently used hydro-ecological models (Tharme, 2003). Habitat simulation models combine hydrological and biological models of habitat selection to determine the variation in habitat use as a function of discharge (Ayllón *et al*., 2012). However, there has been speculation over how accurate these models are at estimating fish populations during periods of low discharge (Beecher *et al*., 2010; Rosenfeld & Ptolemy, 2012).

Westwood *et al*. (2017) reported that flow permanence (river discharge) is the variable with the most influence on the biotic community composition within chalk streams and recommended that a bottom up or site-specific approach is needed to determine accurate ecological discharge thresholds. This project used a unique experimental facility to undertake a large-scale, field-based investigation into the

effects of reduced river discharge on salmonid ecosystems in chalk streams using a bottom up approach.

1.5 Experimental system in Winchester

1.5.1 Study site

The study sites encompassed three cross channels, flowing from the Itchen Navigation Canal to the main River Itchen, near Winchester, Hampshire, UK (51°03°14°N; 1°18°39°W; Figure 1.3). The study streams include Fallodon (length: 223 m, mean wetted width: 5.74 m; Plate 1.1), Blackbridge (length: 190 m, mean wetted width: 6.02 m; Plate 1.2) and Brandy (length: 305 m, mean wetted width: 4.12 m; Plate 1.3). As the streams flow through a nature reserve, towards the River Itchen, they had contrasting riparian vegetation. The upstream section of Fallodon stream contained only a few large trees followed by dense canopy cover in the downstream section. The upstream section of Blackbridge stream consisted of a dense riparian canopy followed by meadow with a few trees. Vegetation along Brandy stream was mainly characterised by a few large trees and bushes, apart from the downstream section where the tree riparian canopy increased. All three streams also had contrasting marginal vegetation. Fallodon had c. 0.5 m of marginal vegetation (width per bank) throughout its length. Due to the wide and shallow nature of Blackbridge it had c. 1.5 m of marginal vegetation that was dominated by emergent aquatic plants. Brandy had the least marginal vegetation, c. 0.2 m, that was dominated by terrestrial plants.

The streams contain well-established communities of aquatic macroinvertebrates and fish, representative of the River Itchen, including wild populations of salmon, and both anadromous and resident brown trout (*Salmo trutta* (Linnaeus, 1758)*;* hereafter trout). Aquatic macrophytes were present within the study streams, submerged *Ranunculus* spp. and emergent *Apium nodiflorum*/*Barula erecta* were the most dominant. Overall, Fallodon had the lowest abundance of macrophytes and Blackbridge has the highest; however, study stream abundances were substantially lower than the main River Itchen.

All three streams draw water from the same source, the Itchen Navigation canal: discharge into each stream was controlled by a single undershot-type sluice gate

(fish are unable to exit the stream via the sluice gate due to the force/speed of the water under the sluice; Plate 1.4). As the streams were fed from the canal, discharges are artificially stable compared with the main river, as the water level in the canal, and therefore the water head difference across the sluice, was maintained for rowing. Consequently, flow type within these streams were predominantly laminar and pool habitats were rare.

Plate 1.1: Upstream section of Fallodon stream.

Plate 1.2: Downstream section of Blackbridge stream.

Plate 1.3: Upstream section of Brandy stream.

River Itchen

Cold stream
(River Itchen tributary)

Itchen Navigation Canal

Un-named stream

Study streams
1) Fallodon
2) Blackbridge
3) Brandy

Sluice gate

End of study reach

Direction of flow

Figure 1.3: Map displaying the location of the different sites and extent of study streams. OS maps accessed 27/02/2019.

Plate 1.4: Brandy sluice gate.

1.5.2 Flow manipulation and data collection

In this study, low summer flow was simulated through reduction in stream discharge by lowering the sluice gate at the top of each stream. Discharge ($m^3\ s^{-1}$) into each of the streams was approximately equal to the area of the sluice gate opening multiplied by the mean water velocity, $[2\ gh]^{0.5}$, where g is the acceleration due to gravity ($9.81\ s^{-1}$) and h the water head difference across the sluice (Beach, 1984). The difference in head was determined by taking readings (twice daily, at approximately 08:00 and 18:00 hours) from depth boards on either side of each sluice gate (see Plate 1.1). Discharge was adjusted to the desired amount by altering the open area of the sluice. The extent of experimental discharge reduction was based on the examination of the variation in mean monthly discharge during the summer (June to September, 1975 to 2018) for gauging stations on the River Itchen and the River Test, a neighbouring chalk stream (see Figure 1.4). Two experimental discharge reduction treatments were chosen: 50% and 90%. An experimental discharge reduction of 50% was chosen as these rivers have experienced similar natural reductions in discharge, whereas an experimental reduction of 90% was chosen because this represents extreme drought, outside the range of variation recorded, that may become more typical in the future due to climate change and increased water abstraction.

The discharge reduction treatments were imposed on the three streams using a temporal block and a Latin square design, such that over three years each stream experienced all discharge treatments (Table 1.2). Stream discharge was then altered to reflect the experimental treatment to which was assigned (Table 1.3). The calculation of discharge (mean and range) was based on twice daily readings from depth boards. A water mixing 'baffle' board was installed immediately upstream of the sluice gates on Brandy and Fallodon to prevent only the relatively cool water from the bottom of the Navigation canal being drawn into the experimental streams during flow manipulations. A baffle board was not needed immediately above Blackbridge sluice as the navigation canal is relatively shallow here and flows steadily, so no temperature stratification occurred.

Figure 1.4: Discharge for each summer month (June to September) as a percentage of overall mean summer discharge, 1975 to 2018. Positive percentages represent summer mean discharges that were higher than the average. Negative percentages represent summer mean discharge that were lower than average. No data available for River Itchen Allbrook 2009 – 2012 inclusive. Data accessed 15/09/2019 from http://www.ceh.ac.uk/data/nrfa/index.html.

Table 1.2: Study design, showing distribution of treatments (C = control, 50% = 50% reduction, 90% = 90% reduction in discharge) in the study streams over three years.

	Year		
Stream	2015	2016	2017
Fallodon	C	90%	50%
Blackbridge	50%	C	90%
Brandy	90%	50%	C

Table 1.3: Mean and (range) of discharge (m^3 s^{-1}) for each stream and treatment over the different sampling occasions for three years.

	2015			2016			2017		
Stream	Fallodon	Blackbridge	Brandy	Fallodon	Blackbridge	Brandy	Fallodon	Blackbridge	Brandy
Treatment	Control	50% reduction	90% reduction	90% reduction	Control	50% reduction	50% reduction	90% reduction	Control
Before	.63 (.59 - .68)	.49 (.46 - .55)	.69 (.63 - .78)	.58 (.48 - .60)	.59 (.54 - .62)	.64 (.52 - .71)	.66 (.59 - .70)	.42 (.36 - .46)	.50 (.44 - .55)
During	.65 (.59 - .68)	.24 (.22 - .26)	.08 (.07 - .09)	.04 (.03 - .04)	.60 (.55 - .64)	.35 (.32 - .47)	.31 (.19 - .33)	.06 (.06 - .07)	.49 (.43 - .53)
After	.66 (.64 - .68)	.52 (.49 - .54)	.67 (.59 - .72)	.59 (.48 - .61)	.59 (.55 - .63)	.67 (.55 - .74)	.62 (.25 - .74)	.43 (.41 - .44)	.49 (.48 - .53)

Within each year, the same experimental timeline was implemented to allow comparisons among years (Figure 1.5). For all three years, the total experimental period lasted for 60 days and started on 21st July 2015, 19th July 2016 and 18th July 2017. Within each experimental period there were three main sampling occasions: before instatement of reduced discharge, during reduced discharge and after discharge reduction once initial discharge had been reinstated. The initial "before" sampling period was followed by an eight-day period to allow fish to recover and to re-establish territories within the stream before fish monitoring, using passive integrated transponder technology, commenced on day 11 using passive integrated transponder technology. Experimental discharge reduction was initiated on day 22-23 and lasted for 25 days. The "during" sampling was carried out on day 43-45, 20 days after the implementation of reduced discharge. Return to pre-manipulation discharge occurred on days 47- 48, 10 days prior to the "after" sampling occasion.

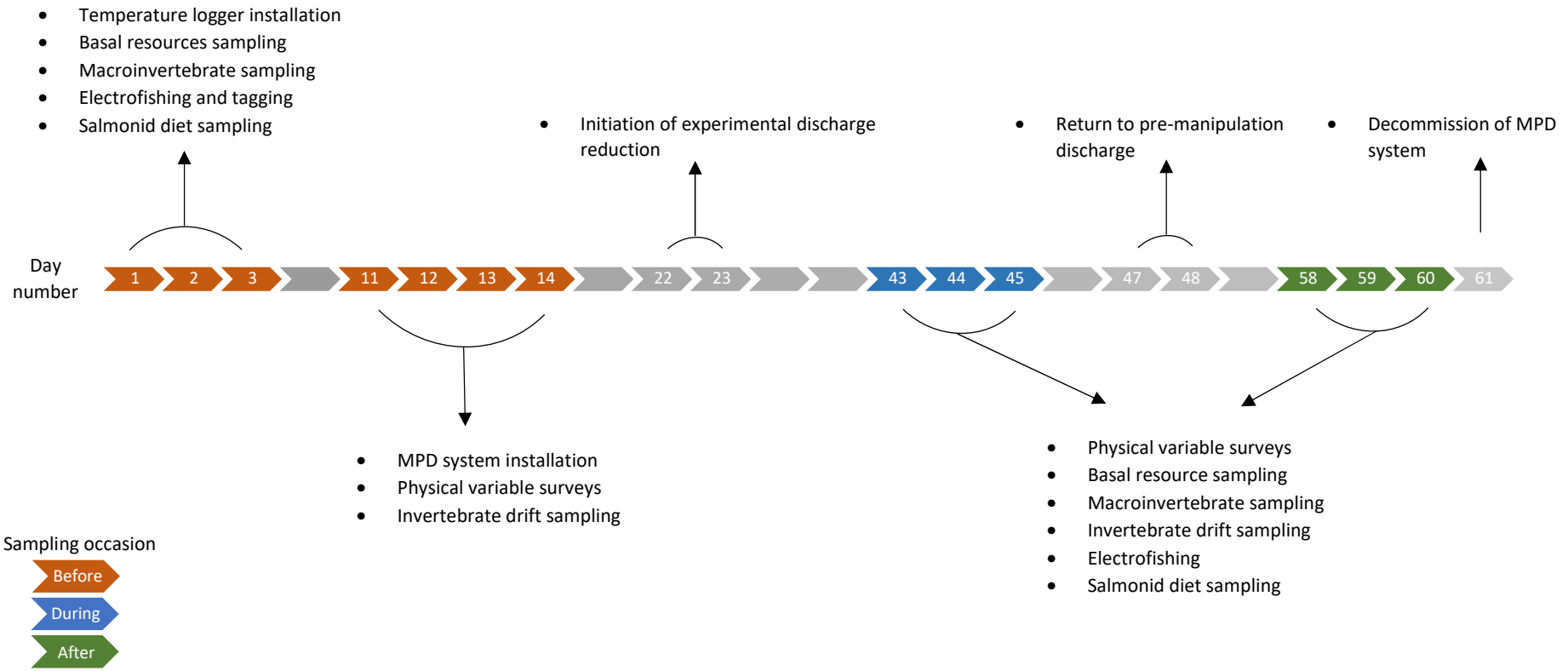

Figure 1.5: Experimental timeline followed for each of the three years. Passive Integrated Transponder Multi point decoder (MPD) systems were used to monitor salmonid habitat use.

1.6 Study aim

The overall aim of this PhD research was to determine the impact of reduced summer discharge, predicted as a result of climate change and an increase in water abstraction, on chalk stream salmonid ecosystems. Specifically, five main subject areas were investigated (see Figure 1.6) and compiled into four discrete but interlinked data chapters. Chapter 2 will outline the effects that the experimentally induced discharge reduction had on the physical characteristics of the streams, as well as basal resources. This chapter will then investigate if there were any changes in the macroinvertebrate community due to the imposed discharge treatments, as well as looking to see if any changes in the abundances of individual taxa can be attributed to the discharge treatments. Chapter 3 will investigate the effects of discharge reduction on the gut contents, consumption rate and prey electivity of salmonids. The findings from the previous chapter (Chapter 2) will be drawn on to explain any differences that may arise. Chapter 4 will identify changes in salmonid habitat use, site loyalty and territory size under reduced discharge conditions, as well as drawing on information from the previous chapters (Chapters 2 & 3) to help explain any changes in habitat use. Chapter 5 will investigate the effects of reduced discharge on growth rate and size (mean length, mass and condition) of salmonids. This chapter will also consider population loss due to the movement of individuals out of the affected stream area under reduced discharge conditions and any affects this may have on population size and density. In addition, findings from the previous chapters (Chapters 2, 3 & 4) will be drawn on to explain any differences that arise. In Chapter 6 ("Overall discussion") the results from Chapters 2-5 are synthesised and evaluated in terms of the overall implications of reduced discharge on salmonid ecosystems. The limitations of this project and potential avenues for further work are also discussed.

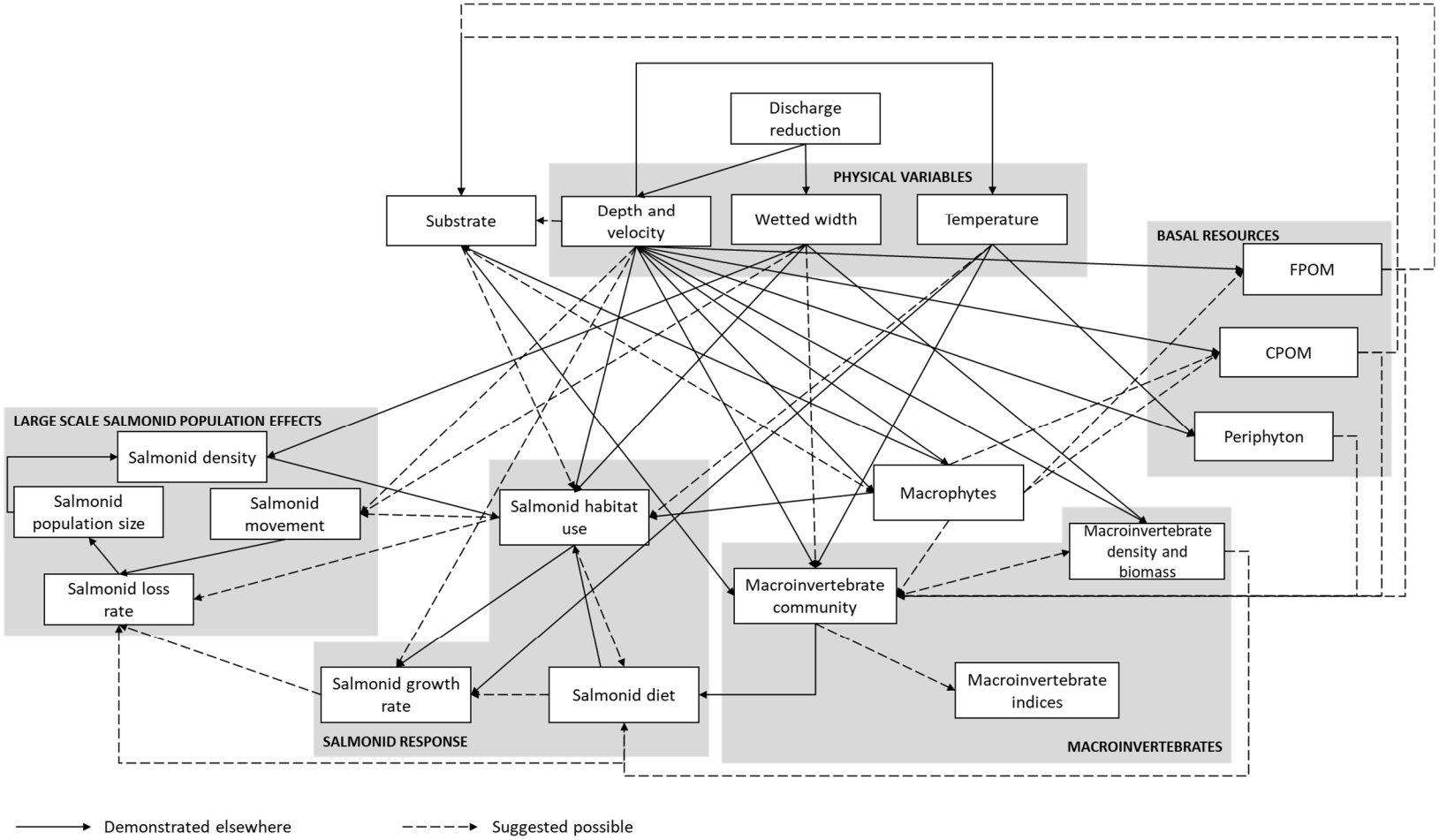

Figure 1.6: Summary of the investigation undertaken here into how reduced discharge may affect the salmonid ecosystem in chalk streams. Grey boxes represent the five main areas that were investigated within this project. Demonstrated elsewhere = studies that provide proof to a link; Suggested possible = studies suggest an indirect/weak influence on the link.

Chapter 2: The effects of experimentally reduced summer discharge on physical characteristics, basal resources and the macroinvertebrate community in chalk streams.

2.1 Introduction

River discharge is widely recognised as the "master variable" controlling key aquatic processes such as habitat (size/area; Poff *et al*., 1997; Richter *et al*., 2003; Poff & Zimmerman, 2010), sediment transport (Wood & Armitage, 1997) and water quality (through dilution and flushing; Poff *et al*., 2010; Wood *et al*., 2010). These processes in turn influence the spatial and temporal distribution and abundance of biota that can persist at a site (Power *et al*., 1995; McKenna *et al*., 2018; Wheeler *et al*., 2018). However, climate change and extensive human water abstraction is predicted to increase the frequency and intensity of short-term summer droughts which will have marked effects on aquatic ecosystems (Johnson *et al*., 2009).

Discharge reduction alters the habitat by reducing water depth, velocity and wetted width (Dewson *et al*., 2007b; House *et al*., 2017), resulting in habitat loss through reduced longitudinal and lateral connectivity (Boulton, 2003; Lake, 2003). However, the effects of reduced discharge on temperature are not as clear. Riley *et al*. (2009a) and Walters & Post (2011) both reported that an experimental discharge reduction, of c. 90% and 50-80% respectively, in summer resulted in negligible changes in stream temperature over c. 100 m. By contrast, Warfe *et al*. (2014) reported that summer stream temperature increased as a result of a c. 59% reduction in discharge, but the increase was strongly dependant on the absence of riparian canopy cover where temperature readings were taken. While it is agreed that discharge reduction will alter all/some of the physical characteristics of a stream, the intensity of the responses will be influenced by the extent of discharge reduction and stream morphology. Discharge reduction will impact naturally wide and shallow streams to a greater extent than streams with narrow and deep channels (Gordon *et al*., 2004; Hauer *et al*., 2013).

Discharge mediated alterations of aquatic habitat will also affect other processes, such as the deposition of suspended fine sediment, including particulate

organic matter (hereafter POM), and accumulation of periphyton biomass (Biggs & Close, 1989; Arrotia *et al*., 2017). There is the potential for the standing stock of organic matter to increase during a period of reduced discharge as reduced water velocity can cause matter to drop out of suspension and any settled matter is less likely to be transported downstream (Walters & Post, 2008). Algal biomass may also increase as a consequence of increased water temperature and light availability associated with decreased water depth (Suren *et al*., 2003), further increasing the potential for retention of fine sediment particles (Jones *et al*., 2014). Such elevated levels of fine sediments, POM and periphyton biomass within the aquatic system can increase blockage of interstitial spaces within the stream bed which serve as important refuges for macroinvertebrates (Bo *et al*., 2007).

Discharge reduction can act as a powerful environmental filter for macroinvertebrates, reducing the habitat area and modifying habitat quality and resource availability (Wills *et al*., 2006; Feld *et al*., 2014). In the initial stages of discharge reduction, macroinvertebrate densities (especially densities of predators) have been reported to increase due to overcrowding within the reduced habitat space (Ledger *et al*., 2013). Decreases in water velocity and surface turbulence can reduce the abundance of taxa that require fast flowing, well oxygenated water, such as some Ephemeroptera, Plecoptera and Trichoptera (Boulton, 2003). As the duration (and intensity) of drought increases, macroinvertebrate density has been reported to reduce by c. 50% (Wright & Berrie, 1987), possibly resulting in a sharp decrease in macroinvertebrate biomass (Walters & Post, 2011). Increased biomass of basal resources, as a consequence of discharge reduction, can influence the macroinvertebrate community (Ledger *et al*., 2013). Increased periphyton biomass and POM can increase the species richness of facultative grazing/shredding taxa (Cuffney & Wallace 1989; Alberts *et al*., 2018), such as gastropods (Jones *et al*., 2000), caddis larvae (Lamberti & Resh, 1983) and amphipods (Ledger *et al*., 2012) over macroinvertebrate predators such as alderflies (Sialidae) and leeches (Hirudinea; Ledger *et al*., 2012), whereas the biomass of collector-gatherer taxa decreased with increased periphyton biomass (Walters & Post, 2011; Dinh & Death, 2018). Overall, changes in the availability of basal resources is likely to lead to a shift in the

community composition of macroinvertebrates (Ledger *et al*., 2013; Aspin *et al*., 2019b). However, rapid recovery of the macroinvertebrate community to pre-drought conditions is possible if the duration of drought has not exceeded a critical point (Boulton, 2003; Boersma *et al*., 2014).

Due to the extensive knowledge of macroinvertebrates and their specific flow requirements, they are widely used to assess the effects of discharge reduction on ecosystem health (Petts *et al*., 2006; Monk *et al*., 2006; Birk *et al*., 2012). Biomonitoring indices have been developed, such as the Lotic-invertebrate Index for Flow Evaluation (LIFE: Extence *et al*., 1999), which is currently used by the UK Environment Agency to assess the impact that discharge reductions have on aquatic ecosystems (Dunbar *et al.*, 2010; Doledec *et al*., 2015). While LIFE can reveal impacts of reduced flow velocities, it is unable to fully capture the impacts of habitat loss during drought. For this purpose Chadd *et al.* (2017) created the Drought Effects of Habitat Loss on Invertebrates index (DEHLI), which places invertebrate families into groups based on their relative tolerance to the loss of suitable habitat at each stage of a reduction in discharge, from the initial disappearance of fast flows to the final loss of all surface water. For both LIFE and DEHLI, a lower score is indicative of greater stress from reduced discharge. Average score per taxon (ASPT) is used to assess organic pollution within the freshwater environment within the UK and across Europe (Clarke *et al*., 2011; Monk *et al*., 2012). Macroinvertebrate samples (family level: Armitage *et al*., 1983) are scored based on their organic pollution sensitivity, where a lower score is indicative of a heavily polluted site (Wenn, 2008). Although originally designed to measure organic pollution, ASPT is increasingly being used to assess other forms of stress on macroinvertebrate communities. For example, Wilding *et al*. (2018) successfully used ASPT (along with other biotic indices) to assess the impacts of flow permanence and drying patterns on the macroinvertebrate community.

The responses of macroinvertebrate taxa to reduced discharge are highly variable between studies, even those of streams of the same classification (e.g. lowland chalk reaches; Westwood *et al*., 2017), and a shift in habitat availability does not necessarily result in community change (Bickerton *et al*., 1993). Any differences in the response between streams could be governed by physical differences (e.g. in

depth, velocity and wetted width; Bickerton *et al*., 1993), the location of streams within the catchment (Jenkins *et al*., 1984), and whether intermittent or perennial streams were sampled as species may have adapted to local variations in discharge (Lytle & Poff, 2004; Stubbington *et al*., 2009). Cortes *et al*. (2002) concluded that community composition in sites that experienced a greater range of discharges varied more than that of sites which experienced less variation in discharge. In contrast, Wood & Armitage (2004), concluded that a reduction in discharge caused a shift towards a simpler community composition compared with non-drought years. However, the macroinvertebrate communities studied by Wood & Armitage (2004) were resilient to the drought such that the community returned to pre-drought composition within a year of experiencing drought conditions.

Many studies have tried to assess the effects of reduced discharge on macroinvertebrates but the literature suggests that, at the stream-scale, these studies are opportunistic (unforeseen drought at the time of sampling), and there is a trade-off between realism and replicability (Harris *et al*., 2007; Ledger *et al*., 2012; Aspin *et al*., 2019a). Current stream-scale surveys of natural drought may not provide a complete picture for a number of reasons: 1) they typically cannot disentangle the effect of discharge from other cofounding drivers, 2) samples are often collected after the event with little or no meaningful baseline data, 3) a lack of replicability, confidence that the same response occurs across other streams is low and 4) the severity of discharge reduction cannot be controlled, making extrapolation of findings to other events and systems difficult. The limitations associated with ad-hoc stream-scale studies explain the growing popularity of mesocosm (i.e. artificial stream channels) experiments, where tight control over environmental conditions can provide a mechanistic understanding of ecosystem responses to extreme events (Taulbee *et al*., 2009; Villeneuve *et al*., 2011; Ledger *et al*., 2013). Although the ability to replicate discharge reduction treatments is an advantage of mesocosms, they inevitably sacrifice some realism and ecological complexity. Mesocosm experiments have lower biological complexity and operate on smaller temporal and spatial scales than natural systems (Petersen & Englund, 2005; Harris *et al*., 2007; Stewart *et al*., 2013), and often lack important characteristics, such as the hyporheic zone, that have proven to be

important refuges during low discharge events (Boulton, 2003). Overall, experimental mesocosms rarely encompass the range of conditions (width, depth, velocity, substrate) that might influence the response to drought, making it difficult for the results to be applied across a natural range of streams. To fully understand the biological interactions that occur, planned experiments at the stream-scale must take precedence. From a management perspective, it is important to make informed decisions based on stream-scale discharge reduction experiments, in order to establish "real world" cause-and-effect mechanisms and allow pertinent planning, preparation and mitigation against the potential negative impacts of reduced summer discharge (Gore *et al*., 2001).

This chapter explores the effects of experimental discharge reduction on the physical characteristics, basal resources and the macroinvertebrate community in three chalk streams on the River Itchen, Hampshire. Each stream had sluice gates at the upstream end which allowed for discharge manipulation. The following hypotheses were tested: 1) Discharge reduction will reduce stream depth, velocity and water wetted width, as well as increase the daily temperature variation, and thus alter the available habitat. 2) Discharge reduction will result in an increase in the standing stock of POM and periphyton on the stream bed. 3) Discharge reduction, will increase macroinvertebrate density and biomass and lead to changes in the community assemblage as sensitive taxa are lost. 4) Any changes in the macroinvertebrate community brought about by discharge reduction will be detected as a decline in the LIFE, DEHLI and ASPT indices. 5) Discharge reduction will produce both immediate (apparent during the reduction) and some lasting (apparent after discharge has been reinstated) effects at the basal resource and macroinvertebrate levels. 6) At each level (basal and macroinvertebrate) differences among the streams will be apparent, due to variations within stream physical characteristics, with the most pronounces effects in the shallowest stream.

2.2 Methods

Data describing the physical characteristics, basal resources and macroinvertebrate communities were collected on all sampling occasions (Before, During and After discharge manipulation) in the experimental study reaches of all three streams (see Figure 2.1) over the three years (excluding the during low discharge sampling occasion in 2015 for basal resources and macroinvertebrates where sample preservation failed; see Chapter 1 section 1.5 for more details on sampling timing and study site).

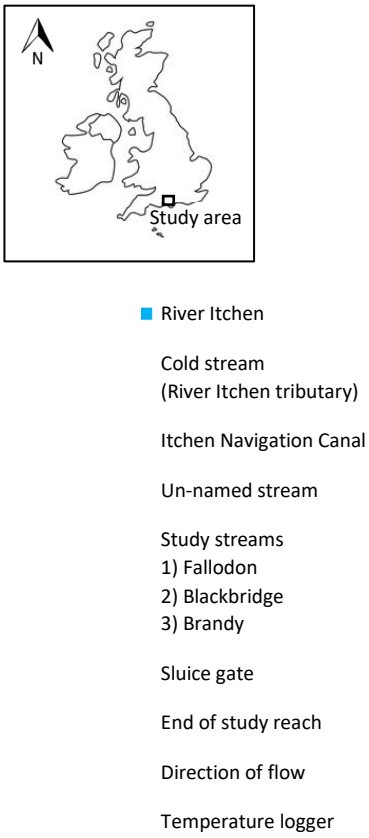

Figure 2.1: Map displaying the location of the different sites, extent of study streams and placement of temperature loggers. OS maps accessed 27/02/2019.

2.2.1 Physical characteristic

On each occasion, water depth and velocity were measured at 16 fixed points within each stream. Measurements were located on the passive integrated transponder (hereafter PIT) multi-point decoder antennae (Plate 2.1; see section 4.2.2 for detailed methods). The measurement points were distributed across the stream in

two transects of five points and one transect of six points. At each point, water depth was measured to the nearest 0.05 m and average velocity was determined over 60 s in mid-water using a Valeport 'Braystoke' BFM002 Current Flow Meter (accuracy: ±0.01 m s^{-1} below 0.5 m s^{-1}; ±2.5% reading above 0.5 m s^{-1}).

Plate 2.1: Example of a velocity measurement being taken with the current flow meter facing in an upstream direction.

The wetted width of the channel was measured to the nearest 0.01 m at 5 m intervals downstream from the sluice gate at the top of each stream. Fixed markers were inserted into the riverbank to allow wetted width measurements to occur at the same location over the study period.

Three Tinytag loggers were deployed in each stream (Gemini Data Loggers U.K. Ltd, Chichester, UK) recording the water temperature (accuracy: ±0.5 °C) every 15 min throughout the study period. The three Tinytag loggers were located (i) in the Itchen Navigation Canal immediately upstream of each sluice gate, (ii) in the upper and (iii) lower sections of each study reach, at similar depths and out of direct sunlight. If Brandy or Fallodon streams were experiencing discharge reduction, baffle boards were installed immediately upstream of the sluice gate to mix the water prior to passing through the sluice to prevent only relatively cool water from the bottom of the Navigation canal being drawn into the streams (see section 1.5.2). All Tinytag loggers underwent a three-point calibration (at 0 °C, 15° C & 20 °C) by Gemini before

deployment. Data collected was adjusted based on calibration error prior to any analysis.

2.2.2 Basal resources and macroinvertebrates

Particulate organic matter and macroinvertebrate assemblages were sampled using a standard Surber sampler (25 x 25 cm, mesh aperture 250 µm) by means of a 30 second disturbance of the river-bed sediment by hand (Wood *et al*., 2010). On each occasion, working in an upstream direction, 10 replicate Surber samples were collected following a stratified-random design in each stream (excluding the rocky pool immediately downstream of the sluice gate). Samples were preserved in 4% formaldehyde and returned to the laboratory.

The material from the Surber samples was passed through 1 mm and 250 µm sieves to separate coarse (>1 mm) and fine (<1 mm but >250 µm) particulate organic matter (CPOM/FPOM) fractions. Macroinvertebrates were separated from the matrix in each fraction by eye, identified under a microscope to the lowest practical taxonomic level (usually species), counted and measured (using a graticule at x10 magnification; see Table A1.1 for dimensions measured and taxa specific length-mass equations used to estimate dry body-mass). Once all macroinvertebrates were removed, the remaining material in the two fractions was dried to constant mass (70 °C, 72 h) and weighed, and then combusted (550 °C, 4 h) and re-weighed to determine ash-free dry mass (AFDM) of FPOM and CPOM (AFDM; difference in mass between dry and combusted weights).

On each sampling occasion, 10 stones were selected randomly from the bed of each stream, and the periphyton removed from a 6 cm x 6 cm area (outlined by a template) of the upper surface using a toothbrush. Using stream water, each sample was washed into individual containers and placed into a dark bag. On return to the laboratory, samples were frozen until they were processed. Once defrosted, the suspension of periphyton was made up to 300 ml using a measuring cylinder and divided into three 100 ml aliquots. One aliquot was filtered through a pre-weighed filter (Whatman GF/C), oven dried to constant mass (70 °C, 72 h) and weighed, and then combusted (550 °C, 4 h) and re-weighed to determine AFDM of periphyton per unit area of stone. The second aliquot was filtered (Whatman GF/C), and chlorophyll *a*

content determined spectrophotometrically after extraction in 90% cold acetone for 24 h (Steinman *et al*., 2017). The third aliquot was preserved with Lugol's iodine for identification and enumeration (results not presented here).

2.2.3 Statistical analysis

Repeated measures analysis of variance (hereafter ANOVA), was used to test the influence of Treatment, Occasion and Stream and the two main interactions (Treatment:Occasion and Treatment:Occasion:Stream; See Table 2.1 for levels within each factor), on water depth, velocity and wetted width using SAS (SAS Institute Inc.). Tukey's post-hoc tests were used to examine differences in means between the two main interactions.

Table 2.1: Break down of factors used within the analysis.

Factor	Factor levels
Year	2015, 2016, 2017
Treatment	Control – no discharge change 50% discharge reduction 90% discharge reduction
Occasion	Before, During, After
Stream	Fallodon, Blackbridge, Brandy
Treatment:Occasion	All Treatment and Occasion factor levels crossed
Treatment:Occasion:Stream	All Treatment, Occasion and Stream factor levels crossed

To determine if reduced discharge influenced water temperature, the difference between the upstream and downstream temperature loggers was calculated at hourly intervals for each stream across the different discharge treatments. The influence of the discharge reduction treatments was determined using General Linear Models (hereafter GLM) in SAS (SAS Institute Inc.), where Stream was treated as a block variable and Treatment, Occasion and Treatment:Occasion were explanatory variables. For Blackbridge stream in 2015, the difference between two upstream loggers (c. 30 m apart) was calculated, due to the loss of the logger deployed in the downstream section.

Analysis of variance based on linear models was used to determine the influence of reduced discharge (Before and During data) and any lasting consequences of the discharge reduction once flow was reinstated (Before and After data) on basal resources, and macroinvertebrate density, biomass and biotic indices, where year was treated as a block (Response ~ Year + Treatment*Occasion – See Table 2.2 question 1 & 2). The same analyses were then run with a Stream interaction included to determine if any differences in the response among the streams were present (Response ~ Year + Treatment + Occasion + Stream + Treatment:Occasion:Stream – See Table 2.2 question 3 & 4). Data were log transformed where necessary to ensure homoscedasticity.

For each Surber sample, the biotic indices LIFE, DEHLI and ASPT (See Table 2.3 for description of each index) were calculated from the macroinvertebrate taxa present. Analysis of variance was used to determine the influence of main effects and interactions. Tukey's post-hoc test was used to examine where differences lay. Analyses of basal resources and univariate measures of macroinvertebrates (density, biomass and biotic indices) were carried out using R-studio version 3.0.3 (R Core Team, 2018).

As the streams were not identical replicates of one another it is possible that their response to the treatments would vary, and so Principle Components Analysis was used to put the difference in response onto a single continuous scale in order to identify any similarities. Principle Component Analysis axis 1 scores were used as a compound variable of the impact of reduced discharge (that replaced all other explanatory variables within the macroinvertebrate univariate analysis), that includes these differences among Streams and Treatment/Occasions based on physical characteristics (water depth, velocity, wetted width and temperature). Analysis of variance based on GLMs was then used to determine if there was an effect of PCA axis 1 score on macroinvertebrate univariate responses.

Table 2.2: Questions asked, data used and explanation of significant explanatory variables. **Bold** represents explanatory interaction terms of interest: if significant differences were attributed to these terms the null hypothesis could be rejected as an experimental effect had been detected.

Question	Occasion data used	Significant explanatory variable meanings
1) Does discharge reduction affect any of the response variables?	Before and During	*Treatment* – There are differences between treatments *Occasion* – There are differences between occasions ***Treatment:Occasion*** – Treatments respond differently over the occasions
2) Are there any lasting effects of discharge reduction on the response variables once discharge is reinstated?	Before and After	
3) Do streams respond differently to reduced discharge for given response variables?	Before and During	*Treatment* – There are differences between treatments *Occasion* – There are differences between occasions *Stream* – There are differences between streams ***Treatment:Occasion:Stream*** – Treatments respond differently over the occasions depending on stream
4) Are there any differences among the streams in terms of lasting effects of reduced discharge on the response variables once discharge is reinstated?	Before and After	

Table 2.3: Description of biomonitoring indices used within the analysis.

Biotic index	Abbreviation	Description
Lotic invertebrate index for flow evaluation	LIFE	Quantifies the effects of drought on instream macroinvertebrate communities by assigning weights to taxa based on recognised velocity associations (Extence *et al*., 1999). Lower numbers are assigned to taxa with slower velocity preferences.
Drought effects of habitat loss on invertebrates	DEHLI	Quantifies the effects of drought on instream macroinvertebrate communities by assigning weights to taxa based on their likely association with key stages of channel drying (Chadd *et al*., 2017).
Average score per taxon	ASPT	Designed to assess the extent of organic pollution, each macroinvertebrate family present is assigned a score based on their sensitivity oxygen availability, and the average score per taxon calculated as a measure of the mean tolerance of the community to oxygen stress (Armitage *et al*., 1983).

Differences in the structure of macroinvertebrate assemblages associated with the factors Treatment, Occasion and Stream were investigated using permutational multivariate analysis of variance (PERMANOVA) in PERMANOVA + for PRIMER software and tested using Monte Carlo tests based on 999 randomisations. PERMANOVA tests to see if there are differences between groups, typically community data, where permutations are used to give accurate *p*-values regardless of the shape and size of the assemblages (Hesterberg *et al*., 2005). If statistically significant, the distribution and abundance of the groups are different. Macroinvertebrate abundance was log transformed to minimise potential effects due to skewed distributions and PERMANOVA was conducted on Bray-Curtis distance dissimilarities. Differences in macroinvertebrate assemblages within Treatment:Occasion and Treatment:Occasion:Stream that were identified by PERMANOVA were presented diagrammatically using multidimentional scaling (MDS).

The relationships between macroinvertebrate assemblages and all environmental variables (see Table 2.4) were analysed using Redundancy Analysis (RDA) using Canoco. To limit excess sample influence and normalise abundances, the data were log transformed. Forward selection using Monte-Carlo tests of 999 randomisations was used to test the significance of environmental variables in explaining differences in the macroinvertebrate assemblages. Environmental variables were only included in the model if $p < 0.01$, where p values were Bonferroni corrected for each additional variable included. Results were presented as a single ordination plot.

Table 2.4: Environmental variables included in the RDA.

Environmental variables	Unit	Type
Year		Categorical
Control		Categorical
50% reduction		Categorical
90% reduction		Categorical
Before		Categorical
During		Categorical
After		Categorical
Control:Before		Categorical
Control:During		Categorical
Control:After		Categorical
50% reduction:Before		Categorical
50% reduction:During		Categorical
50% reduction:After		Categorical
90% reduction:Before		Categorical
90% reduction:During		Categorical
90% reduction:After		Categorical
Fallodon		Categorical
Blackbridge		Categorical
Brandy		Categorical
Depth	cm	Continuous
Velocity	$m\ s^{-1}$	Continuous
Wetted width	m	Continuous
Temperature	°C	Continuous
FPOM	$g\ m^{-2}$	Continuous
CPOM	$g\ m^{-2}$	Continuous
Periphyton biomass	$g\ m^{-2}$	Continuous
Chlorophyll a	$mg\ m^{-2}$	Continuous
Discharge	$m^3\ s^{-1}$	Continuous

2.3 Results

2.3.1 Physical characteristics

General stream characteristics under unmanipulated discharge across all Before occasions in each stream

Fallodon was the shallowest stream, with the second highest velocity, wetted width and downstream temperature increase. Blackbridge was the deepest and widest, with the lowest velocity and greatest increase in downstream temperature. Brandy had the highest velocity, the narrowest width and was the second deepest, and was the only stream that had a decrease in downstream temperature (See Table 2.5). However, care must be taken when interpreting stream depth and velocity as measurements were only taken at 16 locations (the MPD antenna: refer to 2.3.1) which might not necessary represent the stream as a whole.

Table 2.5: Mean (± standard deviation) stream physical characteristics under unmanipulated discharge conditions.

Stream	Depth (cm)	Velocity ($m\ s^{-1}$)	Wetted width (m)	Temperature difference (°C)
Fallodon	10.83 (±6.78)	0.43 (±0.21)	5.74 (±1.31)	0.01 (±0.15)
Blackbridge	21.81 (±12.99)	0.24 (±0.26)	6.02 (±1.39)	0.04 (±0.13)
Brandy	17.08 (±10.51)	0.49 (±0.37)	4.12 (±1.27)	-0.006 (±0.09)

Experimental response

Discharge reduction resulted in a significant difference in water depth, velocity (where measured) and wetted width between treatments (Table 2.6 & Figure 2.2). For all three variables, the two discharge reduction treatments were significantly different in the During occasion compared with the Before and After occasions. Tukey's test indicated that velocity in the During occasion was only significantly different to the Before occasion when a 90% reduction was imposed. Once discharge had been reinstated to pre-manipulation levels, there were no significant differences in water depth, velocity and wetted width compared with Before. Overall, on average, the 90% discharge reduction treatment resulted in a 49% decrease in water depth, 48% reduction in velocity and a 15% reduction in wetted width.

Table 2.6: Results of repeated measures ANOVA on water depth, velocity and wetted width. Factors in **Bold** are of importance.

	Water depth (cm)					Velocity (m s^{-1})					Wetted width (m)				
Between subjects	**df**	**ss**	**ms**	**F**	***p***	**df**	**ss**	**ms**	**F**	***p***	**df**	**ss**	**ms**	**F**	***p***
Treatment	2	355.57	117.78	3.56	*	2	.20	.10	1.96		2	.14	.04	19.11	***
Stream	2	8393	4196.5	84.02	***	2	4.01	2	39.04	***	2	9.58	4.79	1236.7	***
Treatment:Stream	2	1329.53	664.76	13.31	***	2	.24	.12	2.37	*	2	.01	.003	0.82	
Position(Stream)	45	35652.60	792.28	15.86	***	45	19.83	.44	8.57	***	150	16.41	.11	28.25	***
Error	90	4495.20	49.94			90	4.63	.05			298	1.15	.003		
Within subjects															
Occasion	2	2517.79	1258.89	302.14	***	2	1.38	.69	57.97	***	2	.25	.12	214.75	***
Occasion:Stream	4	265.92	66.48	15.96	***	4	.01	.02	2.31		4	.01	.002	4.98	***
Treatment:Occasion	4	1829.60	457.40	109.78	***	4	1	.25	21.19	***	4	.16	.04	70.23	***
Treatment:Occasion:Stream	4	196.48	49.12	11.79	***	4	.06	.01	1.27		4	.002	.001	1.22	
Occasion*Position(Stream)	90	382.50	4.25	1.02		90	1.12	.01	1.05		300	.21	.001	1.20	**
Error(Occasion)	180	750	4.16			180	2.14	.01			596	.34	.001		

Blanks = not significant, ****p <0.001, **p <0.01, *p <0.05.*

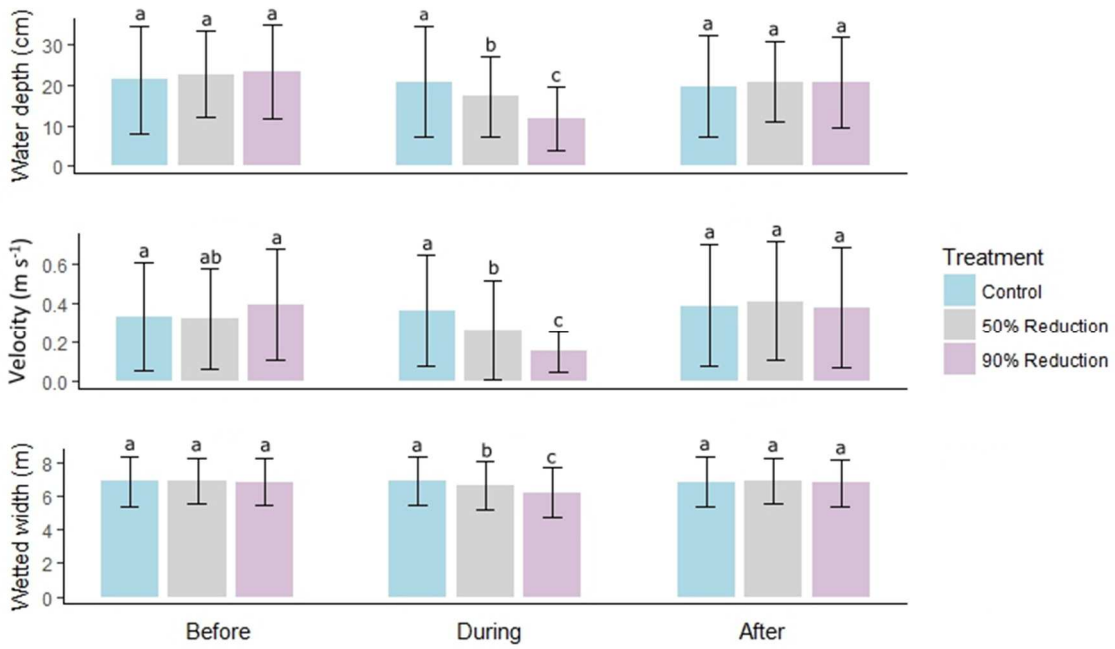

Figure 2.2: Variation in water depth (cm), velocity (m s-1) and wetted width (m) among treatments across sampling occasions (mean ± SD). Results of Tukey's post hoc tests shown, where mean values sharing the same letter are not significantly different.

There was no significant effect of Treatment:Occasion:Stream on velocity and wetted width. Water depth in the three streams responded differently to the experimental manipulation of discharge (Table 2.6). Within the Control treatment, water depth in Blackbridge reduced over the experimental period, with a significant difference between the Before and After sampling occasions, whereas there was no significant difference in water depth in Fallodon and Brandy over occasions (Figure 2.3a). Within the 50% reduction treatment, in Fallodon and Blackbridge there was a significant difference in water depth between the During and both other sampling occasions and no significant difference in water depth between the Before and After sampling occasions, whereas water depth in Brandy did not return to pre-manipulation conditions once the initial discharge was reinstated (Figure 2.3b). Within the 90% reduction treatment, there was a significant difference in water depth between the During occasion and both other sampling occasions in all three streams, and no significant difference in water depth between the Before and After sampling occasions for Fallodon and Brandy, but Blackbridge did not return to pre-manipulation conditions (Figure 2.3c).

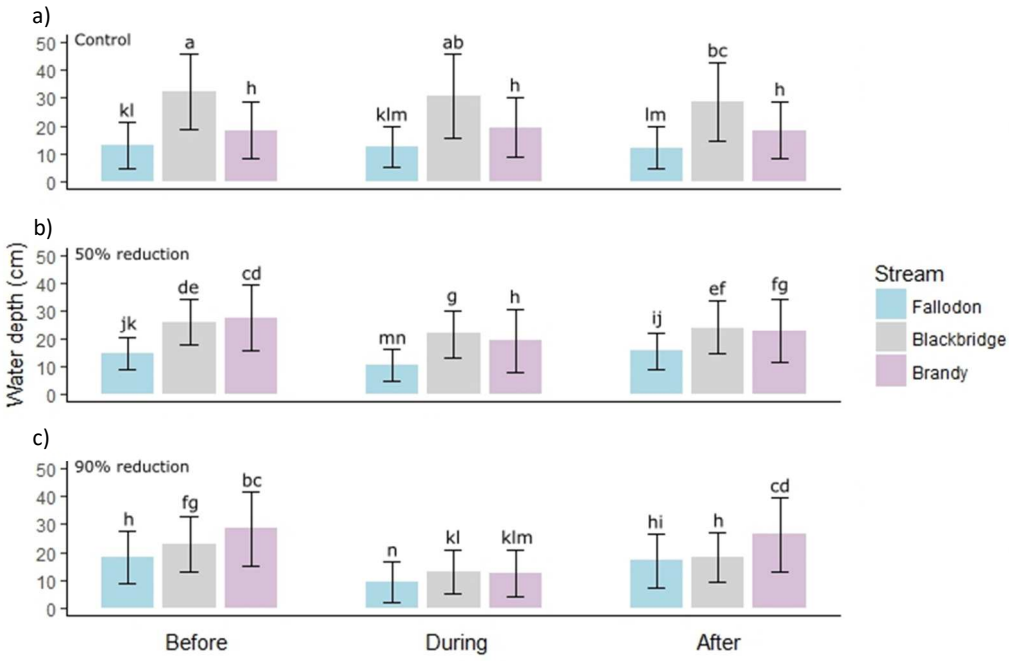

Figure 2.3: Mean (±standard deviation) water depth (cm) in the experimental streams across sampling occasions for each treatment. Results of Tukey's post hoc comparisons shown: mean values sharing the same letter are not significantly different.

Despite the actual differences in temperature being small (less than 0.15°C), discharge reduction resulted in a significant effect on the longitudinal temperature difference in the streams, with the effect most pronounced in the 90% discharge reduction treatment (Table 2.7 & Figure 2.4). Temperature downstream relative to upstream within the During occasion was higher in the reduction treatments compared with the Control, where the downstream temperature tended to be lower than upstream. Similarly, the range of temperature differences was higher in the discharge reduction treatments in the During occasion compared with the Control. Once discharges had been reinstated, longitudinal temperature difference returned to similar pre-manipulation ranges in the 50% reduction treatment but remained slightly elevated within the 90% reduction treatment. The increase in mean temperature difference and temperature difference range within the treatments observed in the During occasion are considered to be the most important aspects of the influence of the discharge reduction on temperature: the discharge reduction treatments caused an increase in water temperature within the streams with the effect becoming more pronounced with progressive reduction of discharge.

Table 2.7: GLM results for longitudinal temperature difference.

Source	df	Type III ss	ms	F	*p*
Stream	2	3.22	1.61	100.25	***
Treatment	2	7.44	3.72	255.54	***
Occasion	2	1.92	.96	66.34	***
Treatment:Occasion	4	2.84	.71	48.92	***
Rep(Treatment:Occasion)	4276	61.42	.01	.90	

Blanks = not significant, ***p <0.001, **p <0.01, *p <0.05.

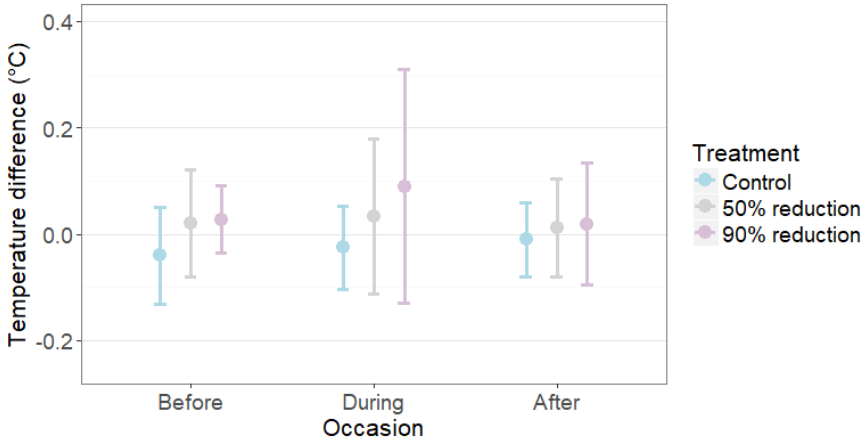

Figure 2.4: Mean (± standard deviation) longitudinal temperature difference between the downstream and upstream loggers for each treatment across the three sampling occasions.

2.3.2 Basal resources

Overall, there was a significant effect of Year on the standing stock of basal resources (Table 2.8 – 2.9). There were no detectable immediate or lasting effects of discharge reduction on periphyton biomass or periphyton chlorophyll *a* (Table 2.8a & Table 2.8b). Furthermore, there were no detectable differences in the response of basal resources among streams in terms of immediate or lasting effects (Table 2.9a & Table 2.9b).

Table 2.8: Statistical results of ANOVA testing the effects of (a) reduced discharge and (b) lasting effects of reduced discharge on basal resources.

	FPOM (g m^{-2})					CPOM (g m^{-2})					Periphyton biomass (g m^{-2})					Chlorophyll *a* (mg m^{-2})				
Source	**df**	**ss**	**ms**	**F**	***p***	**df**	**ss**	**ms**	**F**	***p***	**df**	**ss**	**ms**	**F**	***p***	**df**	**ss**	**ms**	**F**	***p***
a)																				
Year	2	2064.7	1032.3	15.79	***	2	65.52	32.76	33.09	***	2	.33	.16	1.73		2	636.50	318.24	13.29	***
Treatment	2	3.90	1.94	0.02		2	12.21	6.10	6.16	**	2	.53	.26	2.77		2	91.50	45.74	1.91	
Occasion	1	364.4	364.36	5.57	*	1	3.75	3.75	3.79		1	.05	.05	.55		1	78.70	78.67	3.28	
Treatment:Occasion	2	298	148.98	2.27		2	24.33	12.16	12.29	***	2	.07	.03	.40		2	22.50	11.27	.47	
Residuals	142	9284.1	65.38			142	140.56	.99			142	13.78	.09			142	3400	23.94		
b)																				
Year	2	5477	2738.3	13.36	***	2	69.08	34.54	35.03	***	2	27.11	13.55	29.8	***	2	1021	510.89	16.20	***
Treatment	2	1297	648.52	3.16	*	2	6.05	1.53	1.55		2	1.96	.98	2.16		2	34.90	14.47	.55	
Occasion	1	391	391.41	1.91		1	.07	.07	.07		1	.55	.55	1.22		1	3.40	3.38	.10	
Treatment:Occasion	2	622	310.92	1.51		2	.25	.12	.12		2	1.68	.84	1.85		2	25.30	12.65	.40	
Residuals	172	35239	204.88			172	169.59	.98			171	77.69	.45			172	5421	31.52		

****p <0.001, **p <0.01, *p <0.05*, Blanks = *p >0.05*.

Table 2.9: Statistical results of ANOVA testing stream effects of (a) reduced discharge and (b) lasting effects of reduced discharge (b) on basal resources.

	FPOM (g m^{-2})					CPOM (g m^{-2})					Periphyton biomass (g m^{-2})					Chlorophyll *a* (mg m^{-2})				
Source	**df**	**ss**	**ms**	**F**	***p***	**df**	**ss**	**ms**	**F**	***P***	**df**	**ss**	**ms**	**F**	***p***	**df**	**ss**	**ms**	**F**	***p***
a)																				
Year	2	2064	1032	17.51	***	2	65.52	32.76	39.54	***	2	14.56	7.28	12	***	2	636.47	318.24	13.96	***
Treatment	2	3.90	1.94	.03		2	12.21	6.10	7.36	***	2	4.74	2.37	4.01	*	2	91.47	45.74	2.00	
Occasion	1	364.40	364.36	6.18	*	1	3.75	3.75	4.53	*	1	.09	.09	.15		1	78.67	78.67	3.45	
Stream	2	1089	544.59	9.23	***	2	22.83	11.41	13.78	***	2	2.68	1.34	2.26		2	93.79	46.90	2.05	
Treatment:Occasion:Stream	7	535.30	76.47	1.29		7	30.20	4.31	5.20	***	7	3.78	1.82	2.09		7	251.54	35.93	1.57	
Residuals	135	7957	58.95			135	111.85	.82			134	88.18	.59			135	3077.3	22.80		
b)																				
Year	2	5476	2738	17.45	***	2	69.08	34.54	43.95	***	2	27.11	13.55	33	***	2	1021	510.89	17.47	***
Treatment	2	1297	648.52	4.13	*	2	3.05	1.53	1.94		2	1.96	.98	2.46		2	34.90	17.47	.59	
Occasion	1	391	391.41	2.49		1	.07	.07	.09		1	.55	.55	1.39		1	3.40	3.38	.11	
Stream	2	5076	2538	16.17	***	2	22.38	11.19	14.23	***	2	3.20	1.60	4.00	*	2	473.10	236	8.09	***
Treatment:Occasion:Stream	10	5366	536.68	3.42	***	10	20.15	2.01	2.56	**	10	2.84	1.18	2.16		10	238.50	23.85	.81	
Residuals	162	25417	156.90			162	127.31	.78			161	73.33	.39			612	4735	29.23		

****p <0.001, **p <0.01, *p <0.05*, Blanks = *p >0.05*.

Effects of experimental discharge reduction treatments (Treatment:Occasion)

Discharge reduction

There were no detectable effects of reduced discharge on the standing stock of FPOM (Table 2.8a). Discharge reduction resulted in significant differences in standing stock of CPOM between treatments across occasions (Table 2.8a). The standing stock of CPOM was significantly lower in the During occasion within both 50% and 90% reduction treatments compared with the Before occasion whereas there was no change in the control treatment (Figure 2.5).

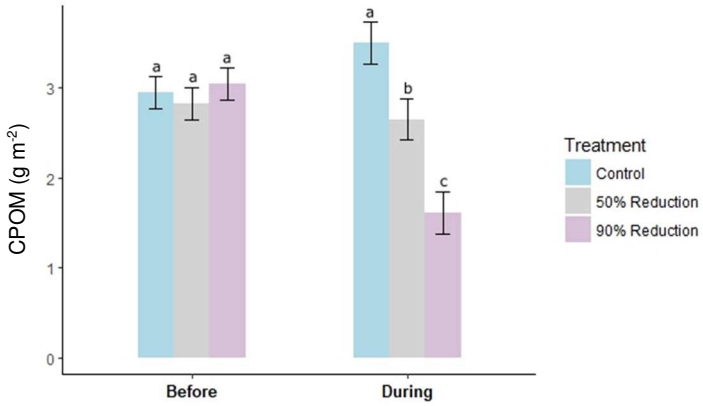

Figure 2.5: Effect of treatments on mean (±standard error) standing stock of CPOM (g m^{-2}). Different letters represent significant differences identified by Tukey's post hoc comparisons.

Lasting effects of discharge reduction

Once the discharge had been reinstated the standing stocks of FPOM and CPOM were not significantly different to those Before the discharge manipulation (Table 2.8b).

Influence of stream (Treatment:Occasion:Stream)

Discharge reduction

There was no detectable influence of stream on the effect of reduced discharge on the standing stock of FPOM (Table 2.9a). A significant interaction between stream and reduced discharge on the standing stock of CPOM across occasions was apparent (Table 2.9a), although none of the differences were explained by the experimental design (Figure A1.1).

Lasting effects of discharge reduction

There was a significant interaction between Stream, Treatment and Occasion in terms of the lasting response of FPOM to reduced discharge (Table 2.9b): there was a significant lasting increase in the standing stock of FPOM within Brandy after 90% discharge reduction which was not apparent in the other streams (Figure 2.6).

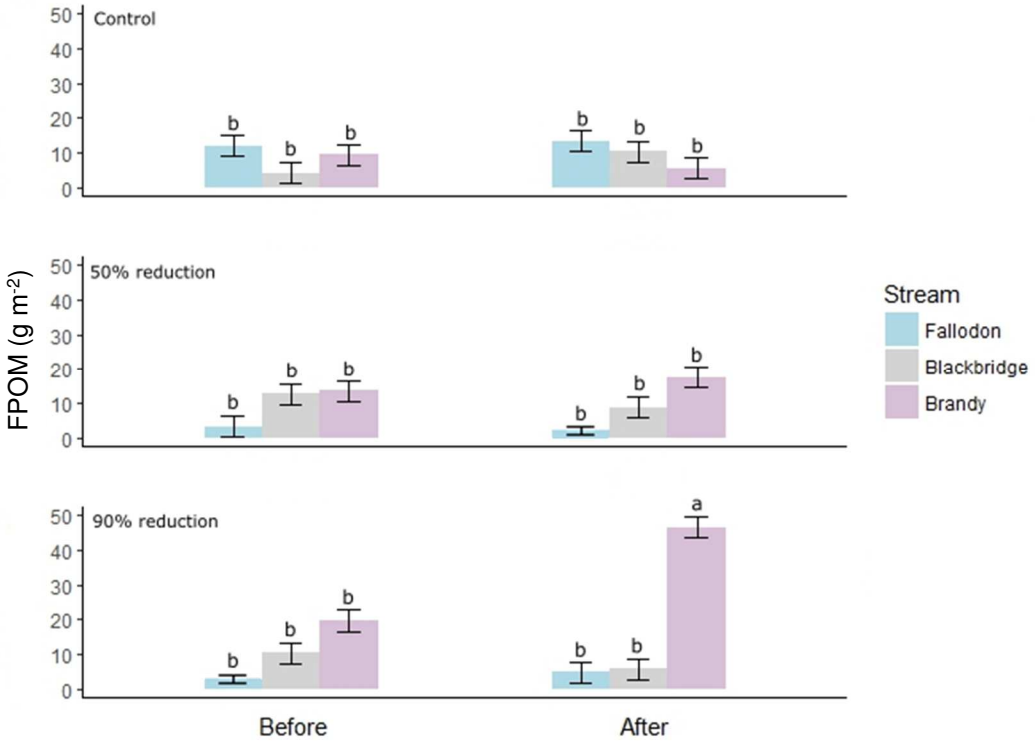

Figure 2.6: Stream specific lasting effects of treatment on mean (±standard error) standing stock of FPOM (g m^{-2}). Different letters represent significant differences explainable by experimental design identified by Tukey's post hoc comparisons. Error bars absent where the mean is smaller than the standard error.

Similarly, a significant interaction was identified between Treatment:Occasion:Stream for the lasting effects of reduced discharge on the standing stock of CPOM (Table 2.9b), although, again, none of the differences were explained by the experimental design (Figure A1.2).

2.3.3 Macroinvertebrate density, biomass and biomonitoring indices

Effects of experimental discharge reduction treatments (Treatment:Occasion)

There were no detectable effects of the experimental manipulation of discharge (Treatment:Occasion) on macroinvertebrate density, biomass and

biomonitoring indices (Table 2.10 & 2.11), although Year and Treatment had a significant effect on the density and biomass of macroinvertebrates.

Influence of stream (Treatment:Occasion:Stream)

The streams were inherently different with respect to macroinvertebrate density, biomass and biotic indices (Stream; Table 2.12 & 2.13). Fallodon consistently had the highest mean density, biomass and biotic indices, whereas Brandy had the lowest. Where significant Treatment:Occasion:Stream interactions were identified, they did not help answer the hypotheses based on the interaction between Treatment and Stream over time (Before/During and Before/After; see Figure A1.3 – A1.8).

Principle Component Analysis

As inherent significant differences among the three streams were apparent for all macroinvertebrate univariate responses, Principle Component Analysis was used to summarise the variation among streams in terms of their response to the discharge reduction treatments. Axis 1 explained 96% of the variation in the physical characteristics of the streams and was strongly associated with water depth (see Figure A1.9). Axis 2 explained an extra 2% which was associated with wetted width. Despite obvious differences in stream characteristics there were no significant relationships between PC axis 1 scores and any of the macroinvertebrate univariate response variables (see Table A1.2).

Table 2.10: Statistical results of ANOVA testing the effects of (a) reduced discharge and (b) lasting effects of reduced discharge on macroinvertebrate density (ind m^{-2}) and biomass (g m^{-2}).

	Density (ind m^{-2})					Biomass (g m^{-2})				
Source	**df**	**ss**	**ms**	**F**	***P***	**df**	**ss**	**ms**	**F**	***P***
a)										
Year	2	24.47	12.23	40.22	***	2	69.57	34.78	34.04	***
Treatment	2	8.31	4.15	13.66	***	2	6.83	3.41	3.34	*
Occasion	1	.12	.12	.40		1	.01	.01	.01	
Treatment:Occasion	2	.59	.29	.98		2	3.73	1.86	1.82	
Residuals	142	43.19	.30			142	145.09	1.02		
b)										
Year	2	36.81	18.40	51.70	***	2	65.30	32.65	29.41	***
Treatment	2	9.24	4.62	12.98	***	2	13.07	6.53	5.89	**
Occasion	1	.09	.09	.27		1	3.16	3.16	2.84	
Treatment:Occasion	2	.86	.43	1.21		2	5.37	2.69	2.42	
Residuals	172	61.22	.35			172	190.91	1.11		

****p <0.001, **p <0.01, *p <0.05*, Blanks = *p >0.05*.

Table 2.11: Statistical results of ANOVA testing the effects of (a) reduced discharge and (b) lasting effects of reduced discharge on biomonitoring indices.

	LIFE					DEHLI					ASPT				
Source	**df**	**ss**	**ms**	**F**	***p***	**df**	**ss**	**ms**	**F**	***P***	**df**	**ss**	**ms**	**F**	***p***
a)															
Year	2	.06	.03	.45		2	.06	.03	5.07	***	2	1.68	.84	2.80	
Treatment	2	.13	.06	.90		2	.03	.03	.61		2	.06	.03	.11	
Occasion	1	.07	.07	.09		1	.03	.03	.05		1	.01	.09	.03	
Treatment:Occasion	2	.05	.02	.03		2	.01	.09	.15		2	.41	.20	.69	
Residuals	142	10.69	.07			142	.86	.06			142	42.61	.30		
b)															
Year	2	.03	.01	.20		2	4.37	2.18	12.64	***	2	4.25	2.12	7.54	***
Treatment	2	.31	.15	2.06		2	.57	.28	1.65		2	.63	.31	1.12	
Occasion	1	.38	.38	5.05	*	1	.01	.01	.11		1	1.28	1.28	4.56	
Treatment:Occasion	2	.02	.01	.19		2	.42	.21	1.21		2	.04	.02	.08	
Residuals	172	12.99	.07			172	29.74	.17			172	48.45	.28		

Table 2.12: Statistical results of ANOVA testing influence of stream on effects of (a) reduced discharge and (b) lasting effects of reduced discharge on macroinvertebrate density (ind m^{-2}) and biomass (g m^{-2}).

	Density (ind m^{-2})					Biomass (g m^{-2})				
Source	**df**	**ss**	**ms**	**F**	***P***	**df**	**ss**	**ms**	**F**	***P***
a)										
Year	2	24.47	12.23	51.52	***	2	69.57	34.78	38.20	***
Treatment	2	8.31	4.15	17.50	***	2	6.83	3.41	3.75	*
Occasion	1	.12	.12	.52		1	.01	.01	.01	
Stream	2	3.13	1.56	6.60	**	2	15.63	15.63	17.16	***
Treatment:Occasion:Stream	7	8.58	1.22	5.16	***	7	7.54	1.50	1.65	
Residuals	135	32.06	.23			135	125.66	.91		
b)										
Year	2	36.81	18.40	64.54	***	2	65.30	32.65	33.88	***
Treatment	2	9.24	4.62	16.20	***	2	13.07	6.53	6.78	**
Occasion	1	.09	.09	.33		1	3.16	3.16	3.28	
Stream	2	3.10	1.55	5.43	**	2	6.38	3.19	3.31	*
Treatment:Occasion:Stream	10	13.79	1.27	4.85	***	10	33.80	3.38	3.50	***
Residuals	162	46.19	.28			162	156.10	.96		

Table 2.13: Statistical results of ANOVA testing influence of stream on effects of (a) reduced discharge and (b) lasting effects of reduced discharge on biotic indexes.

	LIFE					DEHLI					ASPT				
Source	**df**	**ss**	**ms**	**F**	***p***	**df**	**ss**	**ms**	**F**	***P***	**df**	**ss**	**ms**	**F**	***p***
a)															
Year	2	.06	.03	.55		2	1.87	.93	6.56	**	2	1.68	.84	2.95	
Treatment	2	.13	.06	1.11		2	.21	.10	.76		2	.06	.03	.11	
Occasion	1	.07	.07	.12		1	.09	.09	.06		1	.01	.09	.03	
Stream	2	.188	.94	15.43	***	2	4.12	2.06	14.40	***	2	2.47	1.23	4.35	*
Treatment:Occasion:Stream	7	.58	.08	1.36		7	4.00	.57	4.00	***	7	2.17	.31	1.09	
Residuals	135	8.23	.06			135	19.31	.14			135	38.37	.28		
b)															
Year	2	.03	.01	.23		2	4.37	2.18	16.31	***	2	4.25	2.12	7.99	***
Treatment	2	.31	.15	2.41		2	.57	.28	2.13		2	.63	.31	1.19	
Occasion	1	.38	.38	5.89	*	1	.01	.01	.14		1	1.28	1.28	4.83	*
Stream	2	.79	.39	6.17	**	2	4.83	2.41	18.05	***	2	1.63	1.63	6.13	*
Treatment:Occasion:Stream	10	1.73	.17	2.68	**	10	3.61	.36	2.70	**	5	2.20	.44	1.66	
Residuals	162	10.48	.06			162	21.70	.13			168	44.66	.26		

2.3.4 Macroinvertebrate assemblages

PermANOVA indicated that the macroinvertebrate assemblages were significantly influenced by Treatment:Occasion (Table 2.14). The centroids of the treatments separated in the During occasion, despite near complete overlap within the Before and After sampling occasions (Figure 2.7). Sampling occasion, reflected seasonality, overrode any compositional differences due to treatment. PermANOVA also indicated that the macroinvertebrate assemblages were significantly influenced by the Treatment:Occasion:Stream interaction (Table 2.14). Nevertheless, broadly similar patterns of temporal change were followed by each stream in each treatment between occasions, even though the streams were at different locations in ordination space (Figure 2.8). However, during a 90% reduction treatment Fallodon and Blackbridge macroinvertebrate assemblages were very similar indicated by the complete overlap in ordination space.

Table 2.14: Results of PermANOVA indicating significance of experimental effects on macroinvertebrate assemblage structure based on Bray-Curtis dissimilarities.

Source	df	ss	ms	Pseudp – F	P(perm)
Year	2	31010	15505	17.46	***
Residuals	237	2.11	888.18		
Total	239	2.4151E5			
Treatment	2	6536.6	3268.3	5.30	***
Occasion	2	27285	13643	22.13	***
Stream	2	25665	4277.4	6.94	***
Treatment:Occasion	4	4470	1117.6	1.81	***
Treatment:Occasion:Stream	9	42337	4704.1	7.63	***
Residuals	216	1.33	616.4		
Total	239	2.41			

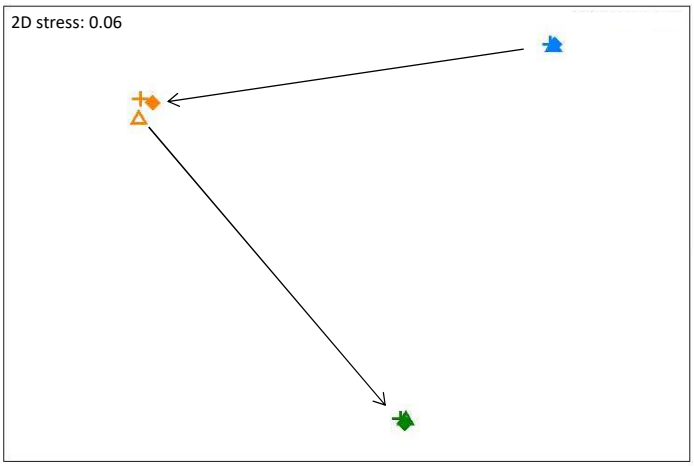

Figure 2.7: Results of MDS ordination showing centroids of samples before (blue), during (orange), after (green) discharge manipulation and control (closed diamond), 50% reduction (open triangle), 90% reduction (cross) flow treatments. Arrows show direction of community change between the different sampling occasions.

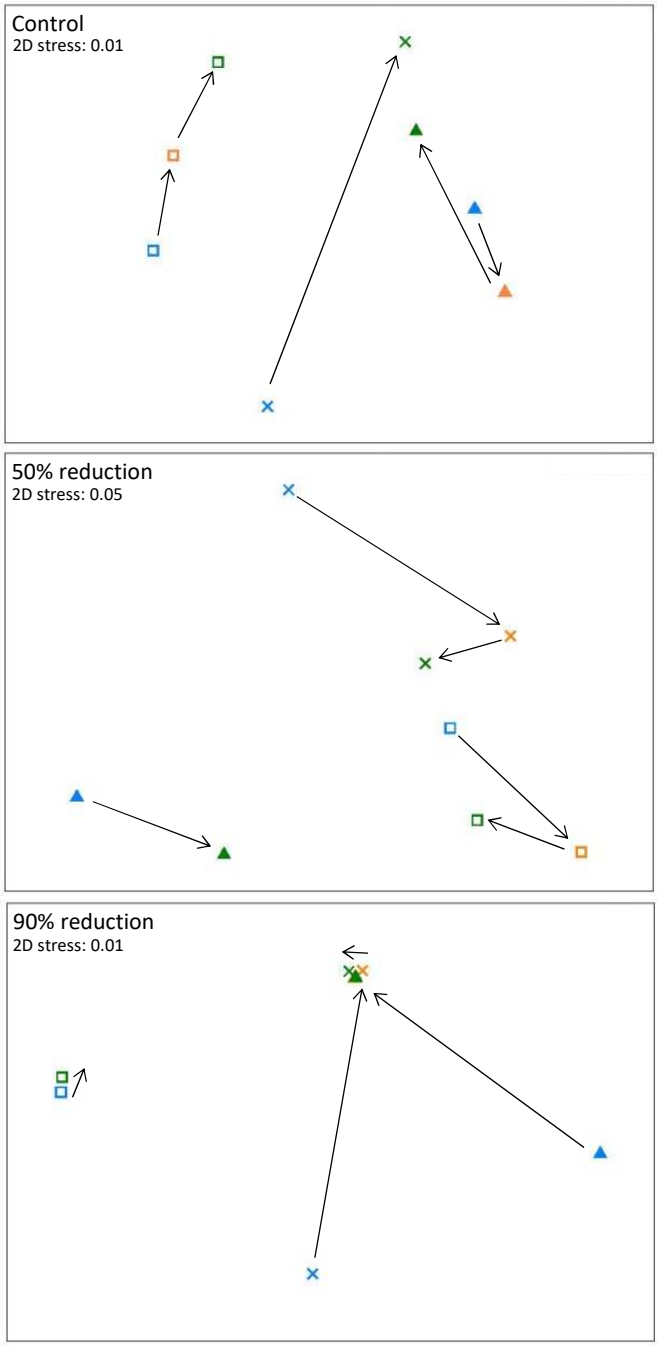

Figure 2.8: Results of MDS ordination showing centroids of before (blue), during (orange), after (green) discharge manipulation in Fallodon (cross), Blackbridge (closed triangle) and Brandy (open square). Arrows show direction of community change between the different occasions. Note: Within the 90% reduction treatment, Backbridge during and after communities are at the same MDS location.

Out of all the environmental variables and interactions of interest, eight variables were identified by RDA as being significant descriptors of the macroinvertebrate assemblage (Figure 2.9). Differences among the three streams were significant in explaining the variation within the macroinvertebrate data, with the assemblages from Brandy being most distinct. For example, *Polycelis tenuis* and *Silo* sp. were generally correlated with Brandy and *Chironomidae* and *Hydroptila* sp. were generally correlated with Blackbridge. Increased abundances of the majority of macroinvertebrate species were correlated with increased water depth, with the exception of a few species.

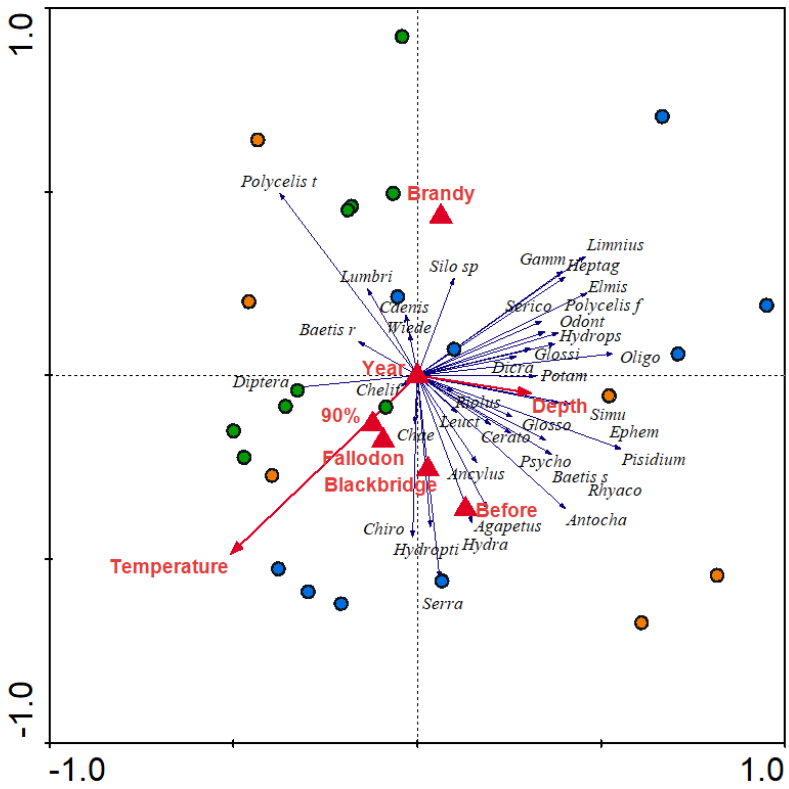

Figure 2.9: Ordination diagram obtained through redundancy analysis (RDA) of the macroinvertebrate taxa in the manipulation experiment to investigate the effects of environmental variables on macroinvertebrate assemblage. Only significant environmental variables identified by forward selection were retained. Samples are coloured by sampling occasion: Blue dots = before, Orange = during, Green = after. Abbreviation: 90% = 90% reduction treatment. Note: replicate samples per occasion overlap each other. For taxa abbreviations see Table A1.3.

2.4 Discussion

Experimental discharge reduction had a clear impact on the physical characteristics of the study streams but had limited effect on the standing stock of basal resources and macroinvertebrate communities. In contrast with what has been reported within the literature from mesocosm experiments (Ledger *et al.*, 2012; Growns *et al*., 2017), the findings of the current suggest that chalk stream biota are highly resistant to short term reductions in summer discharge.

2.4.1 Physical characteristics

As hypothesised, the experimental reductions in discharge caused depth, velocity and wetted width to decrease, and temperature (mean and variation) to increase, with the effect being most pronounced in the 90% reduction of discharge. It can be assumed that groundwater upwelling was negligible as temperature differences did not decrease between the upstream and downstream loggers.

Even though the experimental reduction of discharge produced a significant effect on wetted width, one may have expected the variation in wetted width between treatments to be larger. The results of the experimental discharge reduction presented here agree with Wright & Symes (1999) who reported that, in an English chalk stream, even though discharge decreased substantially, water depth, rather than wetted width, responded more strongly to reduced discharge. This finding contradicts Acreman & Dunbar (2010) who reported that wetted width is the most obvious physical dimention altered when discharge is reduced.

Groundwater-fed chalk streams are known for their relatively stable thermal regimes (Sear *et al*., 1999). Nevertheless, Webb & Zhang (1999) suggested that temperature variation in headwater chalk streams was greatest in the summer due to low discharge and enhanced sensible heat transfer caused by their lower water temperature compared with that of the air. This study found that the discharge reduction treatments caused both mean temperature difference (upstream compared with downstream) and variation in temperature difference to increase over a relatively short distance. Despite the actual differences in temperature being small (less than 0.15°C), both mean temperature and temperature difference increased significantly.

Reduced discharge caused detectable warming of the water in the streams over a relatively short distance, an important finding as, at a catchment scale, this could represent an important difference in temperature, potentially affecting abiotic and biotic processes (Durance & Ormerod, 2009). As most river organisms are ectotherms, changes in temperature have profound effects on their growth, phenology, survival and distribution (Hawkins *et al*., 1997; Daufresne *et al*., 2007).

2.4.2 Basal resources

Basal resources are the key link between physical habitat and primary consumers, providing food as well as micro-habitat (Ledger *et al.*, 2013). This study found that there was no effect of discharge reduction on the standing stock of FPOM. Previous studies have reported increases in the proportion of FPOM that is deposited under reduced discharge, due to an increased rate of settlement of matter out of the water column (Dewson *et al*., 2007b; Walters & Post, 2011). The return of more typical discharge is often associated with an initial increase in the resuspension of FPOM and resultant increased downstream transport of FPOM (Wood & Petts, 1994), and a corresponding decrease in the standing stock of FPOM (Wipfli *et al*., 2007). One possible explanation for discharge reduction having no effect on the standing stock of FPOM within this study concerns the relative importance of sediment delivery (amount arriving) and sedimentation rate (proportion that is deposited). The main delivery of FPOM into the experimental streams was from the Itchen Navigation Canal and the FPOM delivery rate to the experimental stream might have been low, as FPOM may have been deposited within the canal as it was very slow flowing. However, as chalk streams are characterised by having “crystal clear waters” (Sanders *et al*., 2007), indicating a naturally low concentration of suspended material, any increase in the standing stock of deposited FPOM under reduced discharge conditions and once discharge had been reinstated may have been relatively small and difficult to detect. Despite a likely increase in the rate of sedimentation of particles as a consequence of lower stream power in the reduced discharge treatments (Naden *et al*., 2016), the mass of material delivered to the system appears to have dominated the fine sediment dynamics of these streams. This finding is in marked contrast with those of Naden *et al*. (2016), who concluded that, over a wide range of river types, retention was more

important than delivery in determining the mass of deposited fine sediment in streams.

The standing stock of CPOM was significantly lower during the manipulation as a result of experimental discharge reduction. Typically, other studies found that basal resources within the river system, particularly CPOM, increase as the potential energy of the stream is lower and larger particles cannot be transported downstream easily (Anderson & Cabana, 2007; Perkins *et al.*, 2010). However, the season in which discharge reduction takes place is a significant factor in determining the standing stock of CPOM, as reduced stream power will result in increased retention of new terrestrial input. Hence, discharge reduction during leaf fall will have a greater impact on the standing stock of CPOM than during the summer.

The lower standing stock of CPOM during discharge reduction found in this study is likely to be a consequence of reduced supply of CPOM from upstream under reduced discharge. Similar effects (i.e. increased retention) could possibly be seen in real streams experiencing drought as areas downstream would suffer reduced supply if the majority of CPOM is deposited within the upstream areas (Butturini *et al*., 2016; Ejarque *et al*., 2017). Rocky pools directly downstream of the sluice gates in the upper most section of the streams, but outside of the study area, may have been a critical storage area during discharge reduction. During the 50% and 90% discharge reduction treatments, these pools may have had the ability to retain more CPOM as more obstructions would have been encountered due to reduced water depth (Raikow *et al*., 1995; Acuña *et al*., 2004). Thus, when pre-treatment discharge was reinstated, any CPOM stored in the pools (or canal) may have been mobilised (Romaní *et al*., 2013), replenishing the standing stock of CPOM within the reduction treatments such that it was not significantly different to before. Additionally, the majority of CPOM within the streams could have been sourced from the canal and by reducing the discharge via lowering the sluice gate, CPOM delivery from the canal will have been reduced.

In contrast to other studies, there was no effect of discharge reduction on periphyton biomass or chlorophyll *a*. Lake (2003) reported that periphyton biomass and chlorophyll *a* increased during reduced discharge, likely caused by the associated decrease in water depth leading to increased water temperature and light availability.

Dewson *et al*. (2007b) reported that a relationship between water velocity and periphyton biomass might exist, as water velocity affects the colonisation, production and removal of the periphyton community. In addition, grazing macroinvertebrates may reduce periphyton biomass during reduced discharge (Dewson *et al*., 2007b), however, such an effect is highly dependent on the abundance of grazing taxa within the community and their preference to consume periphyton rather than other food types (Chessman *et al*., 2009). Overall, the lack of any significant effect of discharge reduction on periphyton biomass and chlorophyll *a* suggests that the severity of discharge reduction was not strong enough to enhance concentrations in these streams.

2.4.3 Macroinvertebrates

Reduced discharge can affect macroinvertebrate communities by: (1) reducing the physical habitat available due to reduced width (Gippel & Stewardson, 1998; Dewson *et al*., 2007b) and (2) affecting habitat quality over time (Tharme, 2003). Even though the area of wetted habitat available decreased, reduced discharge had no detectable effect on the density or biomass of macroinvertebrates in this study, which does not support the hypothesised reductions with reduced discharge or the findings of other related studies. For example, Bunn & Arthington (2002) suggested that macroinvertebrates are vulnerable to rapid changes in discharge due to the initial loss of physical space, where the magnitude of discharge reduction has been linked to the magnitude of the ecological response (Rolls & Arthington, 2014; Doledec *et al*., 2015). Kakouei *et al.* (2018) used the physical habitat changes brought about by reduced stream discharges, expected as a result of climate change in 2090, in a modelling exercise to predict a potential decrease in species abundance of 42% which will undoubtably affect macroinvertebrate density.

When investigating the effects of an environmental stressor, both spatial and temporal scale are important factors to consider (O'Connor & Cooke, 2015). There are several factors relating to scale relevant to this study that may have prevented a change in macroinvertebrate density or biomass being detected. Firstly, a drought lasting one month may not have been long enough for a significant response of the community to be detected. Secondly, droughts used in mesocosm experiments tend to

be more severe with effects often associated with drying out (but see Jones *et al*., 2015). Within this study, even under a 90% discharge reduction treatment, there was no evidence of stream bed drying and longitudinal habitat connectivity was maintained. According to the findings of James *et al*. (2008a) is crucial for preventing an increase in macroinvertebrate density under reduced discharge conditions, as the available habitat area does not become patchy, which would force invertebrates into a smaller area. In this study macroinvertebrate density was not affected by discharge reduction, which is contrary to a review conducted by Dewson *et al*. (2007b) who reported that, across all river types, when discharge was reduced there was an increase in macroinvertebrate density due to crowding in the reduced area of wetted habitat, followed by a decrease as a result of increased drift, competition and mortality. Although significant, the lack of substantial change in wetted width within this study, even under a 90% discharge reduction, prevented an initial increase and corresponding cascade of effects on macroinvertebrate density. Thirdly, streams are physically more complex relative to those used in mesocosm experiments (Ledger *et al*., 2012), with more available mechanisms to endure the drought. Due to the nature of chalk streams (groundwater dominated), maintenance of wetted habitat allows continued connection with the hyporheic zone. This connection can act as a valuable refuge when surface water discharge is reduced (Boulton, 2003), as long as there isn't a significant increase in fine sediment which can alter macroivertebrate assemblage structure (Jones *et al*., 2015). Macroinvertebrates also use the hyporheic zone to avoid predators (Walters & Post, 2011), and it was likely that this habitat was available as there was no apparent increase in periphyton biomass or FPOM to clog water exchange structures and restrict macroinvertebrate movement in the study streams with reduced discharge (Vadher *et al*., 2015; Vadher *et al*., 2017). In these semi-natural systems, the porosity of the stream bed may have allowed macroinvertebrates of all sizes to use the shallow hyporheic zone as a refuge and, thus, avoid the detrimental effects of the experimental reduction of discharge. Finally, stream communities are relatively complex compared with those used in mesocosm experiments. The streams used in this study originate from the 1700s, whereas mesocosms used in Ledger *et al*. (2012) were colonised for only 2 months prior any sampling so any disturbance effects may have been more pronounced.

This study found that seasonality (sampling occasion) strongly influenced macroinvertebrate community, rather than treatment (see Figure 2.7). This finding compliments the studies of Walters & Post (2008), who reported significant differences in community when comparing different discharge conditions across seasons, and White *et al.* (2018), who concluded that even severe discharge reductions had minimal effect on the biota inhabiting chalk streams. This study found that there were no detectable increases in basal resources during discharge reduction and there were no corresponding increases in shredding or grazing taxa (see Figure 2.9). The macroinvertebrate communities did not follow a clearly defined trajectory in response to moderate (50%) reduction in discharge (Figure 2.8); this finding is consistent with the predictions of Kakouei *et al.* (2018) who showed that changes in discharge led to a variety of responses between streams. Under the 90% reduction, the communities within Fallodon and Blackbridge streams had similar trajectories, possibly as a result of similar physical characteristics (e.g. wetted width, see Table 2.5). It is also possible that, due to the nature of the experimental design, the 90% reduction in discharge resulted in a decrease in the supply of colonists from upstream, which was not as pronounced in the 50% reduction treatment.

Even though stream communities were affected by a 90% discharge reduction, the biomonitoring indices LIFE, DEHLI and ASPT were unable to detect any significant difference as a result of discharge reduction, at the stream and treatment scale. The LIFE index is routinely used by UK regulatory bodies to set water abstraction licence conditions and to track the effect of drought on macroinvertebrate communities. The results from this study clearly indicate that, for chalk stream ecosystems even a month long 90% reduction in discharge might not affect LIFE or even the newly developed DEHLI index. The lack of response in these purpose-built indices questions if it is wise to base abstraction licences solely on macroinvertebrate indices. This is particularly true when the duration of discharge reduction is less than a month, which may not be long enough to produce a detectable effect in these chalk streams, unlike spate rivers (Dunbar *et al*., 2010). However, it is also possible that macroinvertebrate communities have mechanisms that enable them to withstand the impacts of reduced discharge, such as utilisation of the hyporheic zone, which could maintain community

composition (Wood *et al.*, 2010), lessening the impacts of drought (Boulton, 2003). In general, reduction in stream discharge often leads an increase in the proportion of the habitat consisting of pools (Aadland, 1993). It is important to note that due to the relatively homogeneous nature of chalk streams (a lack of pool-riffle sequencing), when the experimental discharge reduction was implemented it did not cause pools to become the dominant habitat type, potentially having a limited effect on the number of macroinvertebrates that are assigned to LIFE and DEHLI reduced flow (pool) classes.

2.5 Conclusion

Reduced discharge treatments resulted in the expected changes in physical characteristics (hypothesis 1 and 5) but did not result in the expected changes in basal resources (hypothesis 2) or macroinvertebrates (hypothesis 3 – 4). Discharge reduction produced few immediate (apparent during the reduction) and lasting (apparent after discharge has been reinstated) effects at the basal resource and macroinvertebrate levels (hypothesis 5). Overall, at each level (basal and macroinvertebrate) stream differences were apparent that seemed to over-ride any higher-level interactions (hypothesis 6).

Controlled mesocosm experiments have provided a detailed knowledge of how aspects of the aquatic ecosystem may respond to extreme events such as reduced discharge (e.g. Ledger *et al*., 2012). However, their lack of realism (such as a metal channel) potentially constrains the possible responses by the community. This might go a long way to explain why the results presented here contrast with work undertaken in mesocosms (Ledger *et al.*, 2012; Jones *et al*., 2015, Growns *et al*., 2017), but are in agreement with Wood & Petts (1994), who concluded that macroinvertebrate communities in chalk streams are resistant to short term droughts. The findings of this chapter provide evidence that stream-scale experiments are highly important, particularly with regards to management decisions. Even though reduced discharge altered physical characteristics in these chalk streams, such effects did not propagate to cause change at higher ecosystem levels. Furthermore, results from this study indicate that stream differences might render “one size fits all” management inadequate. Ideally, management needs to be at the stream level in order to assess ecosystem resistance and resilience such that specific flow management.

Chapter 3: The effects of summer discharge reduction on wild salmon and brown trout diet and prey selectivity

3.1 Introduction

Chalk streams of Southern England have high macroinvertebrate densities, low turbidity and stable summer temperatures making them prime habitat for salmon and trout (Ikediashi *et al*., 2018; Parry *et al*., 2018). However, projected discharge reductions during summer months as a result of climatic change and increased abstraction due to rising water demands threatens these ecosystems (Phang *et al*., 2016). Understanding changes in the diet of salmonids in response to reduced discharge is paramount in order to identify any response thresholds and impacts on growth rate affecting fitness, vulnerability to predation and mortality. In addition, slower growth rates of salmon parr would lead to either smaller smolts (with a lower return rate as adults, see Gregory *et al*., 2018) or a greater proportion of older smolts (impact unknown). In trout, slower growth could also change the propensity to migrate (Jonsson & Jonsson, 1998; Bohlin *et al*., 2001), potentially reducing available prey resources if more fish remain resident.

Both salmon and trout have been extensively studied, which has facilitated a good understanding of their general feeding behaviour, composition of their diet and prey selectivity (Keeley & Grant, 1997; Hyvärinen & Huusko, 2006; Dineen *et al*., 2007; Nunn *et al*., 2012). Salmonids are opportunistic foragers (Weber *et al*., 2014), with diets closely resembling the composition of drift and benthic macroinvertebrate samples (Elliot, 1973; White & Gowan, 2014). They hunt visually for drifting prey whilst selecting foraging sites that enable them to feed in a way that maximises the energetic gains in relation to the energetic costs of capturing, ingesting and digesting prey (Pyke, 1984; Bridcut & Giller, 1995; Rader *et al*., 2007; Johnson *et al*., 2017). Floating terrestrial prey are generally larger than aquatic prey and, therefore, highly conspicuous and susceptible to predation (Baxter *et al*., 2005). As salmonids are engulfers, and therefore gape limited, older fish have been reported to feed predominantly on larger terrestrial prey.

Although drift feeding is the dominant feeding strategy of salmonids, they also adopt alternate strategies, such as benthic foraging (Harvey & Railsback, 2014; Piccolo *et al*., 2014). Benthic foraging is considered by some to be of little importance (Steingrímsson & Gíslason, 2002). However, when environmental conditions are altered such that drift rate is reduced, benthic foraging becomes the dominant feeding strategy (Gunnarsson & Steingrímsson, 2011; Piccolo *et al*., 2014). Reduced discharge and the corresponding decrease in water velocity can result in a reduced rate of delivery of drifting prey (Fausch, 1984; Baker & Coon, 1997; González et al., 2018). Nevertheless, the reduction in area of habitat available may precipitate an initial rise in the number of drifting invertebrates as they seek more suitable habitat conditions, via density dependant emigration (Walters, 1965; Naman et al., 2016).

Piscivory in salmonids, particularly trout, can start from 15 cm in length, once gape size is large enough (Dill, 1983; Kennedy & Greer, 1988; Nakano *et al*., 1999; Keeley & Grant, 2001; Jonsson & Jonsson, 2009). Trout become predominantly piscivorous once they are c.30 cm in length, in order to maintain growth rate and body condition (Kahilainen & Lehtonen, 2002; Steingrímsson & Gíslason, 2002; Hyvärinen & Huusko, 2006).

As well as potentially changing the availability of prey, reductions in discharge will also affect fish habitat and interactions: for example, reduced habitat availability due to a decrease in water depth and wetted width (Dewson et al., 2007b; House et al., 2017; see section 2.3.1), can increase the interactions among salmonid individuals (Warren et al., 2015), leading to greater competition for prey items and higher rates of piscivory by older fish (Smith & Reay, 1991; Keeley & Grant, 2001). Generally, 0+ salmon are stenophagous, with a diet that constitutes largely of Simullidae, Batidae and Chironomidae (Syrjänen et al., 2011; Floury et al., 2018). Nevertheless, the diets of salmonids reflect the micro-habitats they occupy (Sotiropoulos et al., 2006), but within these micro-habitats they are likely to select larger trichopteran prey over smaller Baetidae and Chironomidae (Fochetti et al., 2003). Even though changes in diet may occur due to increased prey availability, Nislow & Armstrong (2012) reported that juvenile salmonids tend to respond to increased prey availability by decreasing the amount of time they spend actively feeding and increasing the time they spend in

refuges, rather than by increasing consumption rates. However, responses to reduced discharge do vary: Gries & Juanes (1998) reported that salmonids essentially abandon all types of foraging during low discharge, whereas Sotiropoulos et al. (2006) reported an increase in the proportion of terrestrial prey in the diet of salmonids under low summer discharge.

Despite numerous studies on salmonid diet, there are no detailed experimental studies investigating the effects of reduced summer discharge. In reporting the first experiment of its kind, this chapter explores the effects of an experimental reduction of discharge on the diet of salmon and trout. In addition, the discussion links the observed diet to the availability of benthic prey (Chapter 2). Three chalk streams where discharge could be manipulated were used in order to test five hypotheses: (1) discharge reduction will decrease the rate of invertebrate drift, (2) the diet of salmonids, as identified from gut contents, during discharge reduction will primarily be prey from the benthos as a result of increased benthic foraging, 3) reduced discharge will be associated with an increase in piscivory by older salmonids, (4) salmonid consumption rates will remain constant under reduced discharge conditions, and (5) salmonid diet response to discharge reduction will vary among streams in a manner that is related to the extent of physical change (which in turn is influenced by the cross-sectional profile of each stream).

3.2 Methods

The investigation took place over three years. In each year, two of the three streams were subject to an experimental discharge reduction (50% or 90%). For information on the study site and discharge manipulation, see section 1.5.

3.2.1 Salmonid capture

During each of the three sampling occasions (Before, During and After discharge manipulation: see Figure 1.5) electrofishing (Control box EFU-1, East Anglian Electrical Services; operational settings: 150V; 20% pulsed duty cycle; 40Hz, anode diameter 40 cm and length of cathode 4 m) was used to capture fish within defined sections in the three study streams (Figure 3.1). Captured fish were anesthetised (2-phenoxy-ethanol), weighed (to nearest 0.1 g) and fork length measured (to nearest

mm). The fish were then left to recover for c. 2 hours before being returned to the site of capture. All procedures were carried out by licenced personnel under the authority of Home Office Project Licence 70/7958. All recorded fish were aged using length frequency analysis.

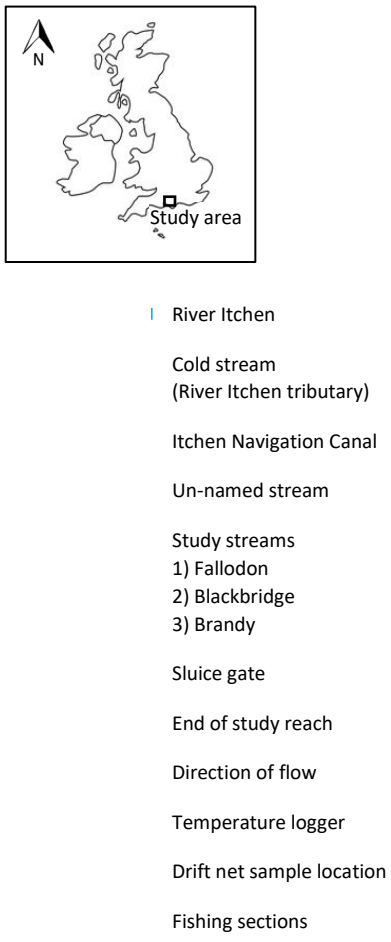

Figure 3.1: Map displaying the location of the different sites, extent of study streams, location of temperature loggers, placement of drift nets and predefined electrofishing sections. OS maps accessed 27/02/2019.

3.2.2 Gut contents

Within each electrofishing survey, a sub-sample of individuals (salmon and trout) in each age class (0+, 1+ and ≥2+) were gut flushed using a modified version of the Seaburg (1957) technique (Twomey & Giller, 1990). During gut flushing the fish were held ventral side up with their head tilted slightly downwards, tubing was inserted into the mouth and the gut contents from the foregut was back flushed with stream water using a foot pump. This sampling procedure was non-destructive and has

no significant lasting effects on fish feeding, condition or behaviour (Twomey & Giller, 1990). The gut contents from each individual were collected in a sampling tray, passed through a 250 µm sieve, placed into individual sample pots and preserved in c. 10% formaldehyde.

On return to the laboratory, samples were washed and prey items identified to the lowest practical taxonomic level, usually family (higher taxonomic resolution was rarely possible due to partial digestion), and digestion resistant body parts measured using a dissecting microscope with an ocular micrometer in order to estimate mass (See Table A2.1 for dimensions measured and taxa specific length-mass equations used to estimate dry body-mass). Simple rules were used to determine the minimum number of individuals consumed where specimens were broken up. Any unidentifiable material was excluded. Where possible, the gut contents from 20 individuals per species/cohort were identified within each stream for each occasion every year. The `Specaccum` function of R, within the vegan package (Oksanen *et al*., 2013), was applied to create species accumulation curves for each species/cohort. Identified prey needed to represent ≥ 85% of estimated total prey richness to ensure that the diet was representative of the sampling occasion for each species/cohort. If the 85% threshold was not met with 20 individuals, additional samples were processed where available. In total 1904 (384 salmon and 1503 trout) individual stomach contents were analysed.

3.2.3 Prey availability sampling

Surber and drift net samples were collected to quantify the availability of prey in the environment (± 5 days of gut flushing). For a detailed description of Surber sampling and the associated laboratory protocol see section 2.2.2. To quantify the availability of prey in the drift, four drift net traps (aperture 25 x 40 cm, mesh size 250 µm) were set within each stream (see Figure 3.1 for drift net sample location) approximately 1 hour before sunrise and left in place for a period of approx. 3 hours within the During occasion for each experimental year (2015, 2016 and 2017). Nets were placed horizontally across the stream and each secured using two 0.5 m steel rods (Plate 3.1). Care was taken to ensure each net covered the vertical water column including the surface of the water to catch terrestrial drift. Water depth (m) and

velocity (m s^{-1}), using a Valeport 'Braystoke' BFM002 Current Flow Meter (accuracy: ±0.01 m s^{-1} below 0.5 m s^{-1}; ±2.5% reading above 0.5 m s^{-1}), were measured in front of each net. On removal, net contents were transferred into individual sample pots and preserved in c. 10% formaldehyde. On return to the laboratory, samples were washed, and prey items identified to the lowest practical taxonomic level (usually genus for aquatic and family for terrestrial items), measured (as above) and counted.

Plate 3.1: Example deployment of drift nets within Blackbridge stream.

3.2.4 Data analysis

Drift rate

Drift rate was calculated to assess the effect of discharge reduction on the delivery of prey. Firstly, the total volume of water that was filtered through each drift net was calculated:

$$Total\ water\ filtered\ (m^3) = Water\ depth\ (m)\ x\ Drift\ net\ width\ (m)\ x\ Velocity\ (m\ s^{-1})\ x\ Time\ (s) \quad (1)$$

Where water depth and velocity are from individual net recordings taken during deployment and time represents the duration of deployment. For each net, the abundance and biomass of macroinvertebrates (total/aquatic/terrestrial) caught were

then calculated to obtain the density of each macroinvertebrate measure (total abundance of individuals used as an example):

$$Total\ density\ (ind\ m^{-3}) = \frac{Total\ abundance\ (ind)}{Total\ water\ filtered\ (m^3)} \quad (2)$$

Finally, delivery of drifting prey was calculated for each net, where stream discharge represents the discharge within the During sampling occasion (see Table 1.3):

$$Delivery\ rate\ (ind\ s^{-1}) = Total\ density\ (ind\ m^{-3})\ x\ Stream\ discharge\ (m^3\ s^{-1}) \quad (3)$$

Two-way ANOVA based on linear models was then used to assess the effects of Year and Treatment*Stream on the rate of delivery of macroinvertebrates (total/aquatic/terrestrial) in terms of abundance and biomass. The data were log and log+1 transformed as necessary.

Gut contents

The influence of reduced discharge and any lasting effects on salmonid gut contents were investigated (see Table 2.2 – for explanation of statistical models used to determine the effects of discharge reduction and lasting effects of discharge reduction). Specifically, ANOVA, based on linear models, with Tukey's post hoc tests were used to examine differences in the abundance, richness (number of different prey taxa), and total biomass of prey and the proportion of biomass that comprised terrestrial prey taxa in the gut contents of salmonids. The analysis was carried out to determine the influence of treatments on the change over time between the Before and During sampling occasions (discharge reduction), and the Before and After sampling occasions (lasting effects), such that the Treatment:Occasion interaction was of specific interest. The analysis was then repeated to include the individual streams as a factor, where the interaction (i.e. Treatment:Occasion:Stream) would determine if there was any significant differences in the response of salmonid diet among the different streams (see Table 2.1 & 2.2 – for breakdown and explanation of experimental factors and interactions).

The `Manyglm` function of R within the mvabund package (Wang *et al*., 2012) was used to determine if the experimental manipulation affected the abundance of individual taxa found in salmonid gut contents. `Manyglm` fits a separate, univariate, generalized linear model to the abundance of each taxon (in this case counts of the taxon in each gut) and relates each abundance to a common set of explanatory variables (Treatment*Occasion) to create a multivariate analysis across taxa. The `Manyglm` model was applied to each salmonid species and cohort separately, using the count of individuals of each taxon present within the gut as response variables, and Treatment, Occasion and Treatment:Occasion as explanatory variables. Means were calculated where a significant influence of Treatment:Occasion on abundance was identified.

Consumption rate

The rate of consumption of prey by salmonids, φ, was calculated using the formula of Speirs *et al*. (2000):

$$\varphi = \frac{n}{t} \tag{4}$$

Where t = residence time and n = number of prey individuals in the gut. Residence time (t) is dependent upon an exponential relationship with temperature (Elliott, 1972):

$$t = \alpha e^{-bT} \tag{5}$$

Where T = temperature (°C) and a and b are constants. Therefore, the following equation was used to calculate the rate of consumption of individuals per day:

$$\varphi\ individuals = \frac{n}{\alpha e^{-bT}} \tag{6}$$

To determine the rate of consumption in terms of biomass, mg consumed per day was calculated using equation (6) where n was substituted with total biomass. Consumption rate in terms of individuals and biomass were calculated to determine any relationships. For example, if fish consume more individuals but biomass does not increase, fish are consuming a greater number of smaller prey. Whereas if fish consume the same number of individuals but biomass increases, fish are consuming

larger prey items. If both consumption of individuals and biomass increase (decrease) then fish are consuming more (less). In each stream a Tinytag logger (Gemini Data Loggers U.K. Ltd, Chichester, UK) within the upper reach of the study streams recorded water temperature (accuracy: ±0.5 °C) every 15 min throughout the study period (see Figure 3.1 for Tinytag location). Mean temperatures were calculated for each stream, occasion and treatment and used in equation 6. Residence time constants a and b were 1936 min and -0.112, respectively, which were derived from Elliott's 1972 study of brown trout. To use the equation, as set out in Elliott (1972), it was assumed that a minimum of 25% of the total mass of a prey item had to remain for it to be identifiable. Rate of consumption, as number of individuals and mg per day, was analysed using the same statistical approach as was used for gut contents.

Electivity of prey

Ivlev's Electivity Index (Ivlev, 1961) was calculated as a measure of prey preference by salmonids relative to the abundance of prey in the environment. In this case, the mean relative abundance of macroinvertebrates in the benthos (Surber samples) and drift samples, on each occasion for each treatment, were used as a measure of availability. Ivlev's Electivity Index was calculated as:

$$Ei = \frac{(ri - ni)}{(ri + ni)} \quad (7)$$

Where *Ei* = electivity for the i^{th} taxon, *ri* = the relative abundance of that taxon in the diet, and *ni* = the relative abundance of that taxon in the environment (benthos or drift). Values range from −1 to 1, where −1 indicates total prey avoidance, 0 indicates that an item was taken in proportion to its relative abundance in the ecosystem, and 1 indicates total prey preference (Ivlev, 1961).

As relatively few salmon were caught, the data from 0+ and 1+ age classes were pooled in the analysis: previous studies have found considerable overlap in the diet of these two age classes in this species (Dineen *et al*., 2007). All analyses were carried out in R-studio version 3.0.3 (R Core Team, 2018).

3.3 Results

Overall drift samples contained 36 different taxa. Chironomidae were the most abundant (39%), followed by Simuliidae (14%), Baetidae (12%) and *Gammarus pulex* (Linnaeus, 1758; 10%). There were no significant effects of discharge reduction on the delivery rate of either invertebrate abundance or biomass (total, aquatic or terrestrial), within the During sampling occasion (Table A2.2, Figure A2.1 & A2.2). Significant differences between streams were detected (Table A2.2), Tukey's post hoc tests identified that Fallodon drift contained lower total abundances compared to Brandy as there were fewer aquatic individuals within the drift.

The response of salmonid diet (gut content) and consumption rate to discharge reduction and lasting effects of discharge reduction differed significantly between streams (Table A2.3 - Table A2.5, respectively). Where significant Treatment:Occasion:Stream interactions were identified, they were inconsistent and did not vary among streams in a manner that were related to the extent of physical change (see Figure A2.3 – A2.6 for salmonid diet examples). For instance, even when experiencing the same physical change in Brandy (90% discharge reduction), species/cohort consumption rate (individuals and biomass) were variable (see Figure A2.7– A2.9).

3.3.1 Salmon

Effects of experimental discharge reduction treatments

There was no detectable experimental effect of reduced discharge on the abundance, richness or measures of biomass consumed by salmon (Table 3.1). However, lasting experimental effects of reduced discharge on salmon diet were detected (Table 3.2). Abundance and total biomass of prey in the guts of salmon that experienced either a 50% or 90% reduction increased significantly over time compared with the Control, which did not change (Figure 3.2 & 3.3). Prey species richness in the guts of salmon that experienced the 50% reduction treatment increased significantly over time whereas the other two treatments did not (Figure 3.4).

Abundance of individual prey taxa within the gut (Treatment:Occasion)

Mvabund analysis of the influence of the experimental design on the abundance of prey in the guts of salmon identified significant effects for Simuliidae larvae (Table 3.3). During the 50% discharge reduction, salmon had more Simuliidae larvae in their guts than Before, whereas the guts of salmon from the Control and 90% reduction treatments contained fewer. The mean abundance of Simuliidae larvae in the guts of salmon was highest in the After occasion for all treatments. In addition, there were practically no Simuliidae in the guts of salmon During 90% discharge reduction.

Consumption rate

There were no detectable effects of the experimental discharge reduction, or any lasting effects, on the rate of consumption of individuals and biomass by salmon (Table 3.4).

Electivity of prey

Consistent with the results of the mvabund analysis, salmon appeared to select Simuliidae larvae from the benthos During the 50% discharge reduction compared with the other treatments (Figure A2.10). Salmon also selected terrestrial prey taxa (Figure A2.10 & A2.11).

Table 3.1: Statistical results of ANOVA testing the effects of reduced discharge on salmonid diet.

	Abundance					Richness					Total biomass					Proportion of terrestrial biomass				
Source	**df**	**ss**	**ms**	**F**	***p***	**df**	**ss**	**ms**	**F**	***P***	**df**	**ss**	**ms**	**F**	***p***	**df**	**ss**	**ms**	**F**	***p***
Salmon																				
Year	2	10.78	5.39	2.93		2	3.01	1.50	4.36	*	2	17.86	8.93	2.42		2	.005	.002	1.05	
Treatment	2	42.51	21.25	11.57	***	2	1.28	.64	1.86		2	18.50	9.25	2.50		2	.001	.001	.27	
Occasion	1	39.96	39.96	21.75	***	1	.39	.39	1.14		1	52.64	52.6	14.26	***	1	.005	.005	2.05	
Treatment:Occasion	2	6.77	3.38	1.84		2	.52	.36	.76		2	1.80	.90	.24		2	.009	.004	1.77	
Residuals	236	433.46	1.83			236	81.21	.34			236	867.03	3.68			236	.643	.002		
0+ trout																				
Year	2	6.41	3.20	4.17	*	2	5.25	2.62	8.38	***	2	7.65	3.82	1.67		2	.003	.0019	5.73	**
Treatment	2	1.61	.80	1.04		2	2.52	1.25	4.01	*	2	4.84	2.42	1.06		2	.001	.0006	2.01	
Occasion	1	4.81	4.81	6.25	*	1	.14	.14	0.47		1	56.49	56.5	24.76	***	1	.004	.0047	14.30	***
Treatment:Occasion	2	1.31	.65	.85		2	.91	.45	1.45		2	17.86	8.92	3.91	*	2	.001	.0001	.03	
Residuals	410	315.30	.76			410	128.51	.31			410	930.58	2.28			410	.136	.0003		
1+ trout																				
Year	2	6.15	3.07	3.83	*	2	7.17	3.58	10.49	***	2	49.54	24.8	5.78	**	2	.003	.0015	2.67	
Treatment	2	.87	.43	.54		2	.89	.44	1.30		2	5.94	2.96	.69		2	.001	.0007	1.35	
Occasion	1	.15	.14	.18		1	.20	.20	.60		1	54.68	54.7	12.76	***	1	.014	.0148	25.42	***
Treatment:Occasion	2	6.50	3.25	4.05	*	2	3.31	1.65	4.85	**	2	2.35	1.17	.27		2	.003	.0019	3.30	*
Residuals	396	317.67	.80			396	135.29	.34			396	1688.1	4.28			396	.230	.0005		
≥2+ trout																				
Year	2	2.83	1.41	1.90		2	3.65	1.82	5.13	**	2	50.82	25.4	4.45	*	2	.183	.091	1.76	
Treatment	2	8.70	4.35	5.84	**	2	1.20	.60	1.69		2	62.67	31.3	5.49	**	2	.180	.090	1.73	
Occasion	1	.02	.02	.03		1	1.05	1.05	2.95		1	43.67	43.6	7.65	**	1	.382	.382	7.35	**
Treatment:Occasion	2	3.81	1.90	2.56		2	1.40	.40	1.97		2	7.49	3.74	.65		2	.003	.004	.08	
Residuals	224	166.13	.74			224	79.76	.35			224	1254.5	5.70			224	11.433	.051		

****p <0.001, **p <0.01, *p <0.05*, Blanks = *p >0.05*.

Table 3.2: Statistical results of ANOVA testing the lasting effects of discharge reduction on salmonid diet.

	Abundance					Richness					Total biomass					Proportion of terrestrial biomass				
Source	**df**	**ss**	**ms**	**F**	***p***	**df**	**ss**	**ms**	**F**	***P***	**df**	**ss**	**ms**	**F**	***p***	**df**	**ss**	**ms**	**F**	***p***
Salmon																				
Year	2	40.40	20.20	9.61	***	2	2.40	1.20	3.97	*	2	.79	0.39	0.14		2	.004	.002	.68	
Treatment	2	10.35	5.17	2.46		2	2.82	1.41	4.67	*	2	11.19	5.59	2.01		2	.005	.002	.91	
Occasion	1	140.06	140.05	66.69	***	1	1.42	1.42	4.71	*	1	53.92	53.9	19.46	***	1	.001	.001	.34	
Treatment:Occasion	2	24.02	12.01	5.71	**	2	1.85	.92	3.05	*	2	34.15	17.1	6.16	**	2	.001	.001	.01	
Residuals	264	554.41	2.10			264	79.85	.30			264	731.43	2.77			264	.769	.002		
0+ trout																				
Year	2	.86	.85	1.09		2	5.90	2.95	10.42	***	2	1.39	1.38	.65		2	.0029	.0014	6.64	**
Treatment	2	1.68	.83	1.07		2	2.94	1.47	5.20	**	2	20.84	10.4	4.94	**	2	.0006	.0003	1.53	
Occasion	1	6.96	6.96	8.89	**	1	1.97	1.97	6.97	**	1	4.00	4.00	1.89		1	.0005	.0001	2.49	
Treatment:Occasion	2	1.07	.53	.68		2	2.91	1.45	5.15	**	2	7.22	3.60	1.71		2	.0001	.0001	.12	
Residuals	421	329.30	.78			421	118.80	.28			421	880.86	2.10			421	.0930	.0002		
1+ trout																				
Year	2	9.55	4.77	5.82	**	2	5.92	2.96	8.16	***	2	30.52	15.3	3.92	*	2	.0139	.0069	14.09	***
Treatment	2	1.9	.96	1.17		2	1.49	.74	2.06		2	20.27	10.1	2.60		2	.0011	.0005	1.20	
Occasion	1	3.64	3.64	4.44	*	1	.34	.34	.95		1	74.11	74.1	19.06	***	1	.0035	.0035	7.19	**
Treatment:Occasion	2	4.80	2.39	2.92		2	.46	.23	.64		2	8.01	4.00	1.03		2	.0005	.0002	.56	
Residuals	411	337.04	.82			411	149.01	.36			411	1590.1	3.88			411	.2029	.0004		
≥2+ trout																				
Year	2	7.39	3.68	5.13	**	2	4.40	2.20	6.17	**	2	100.87	50.4	11.32	***	2	.13	.06	1.68	
Treatment	2	9.40	4.70	6.53	**	2	3.85	1.92	5.40	**	2	54.91	27.5	6.16	**	2	.33	.16	4.18	*
Occasion	1	1.41	1.41	1.96		1	4.25	4.25	11.9	***	1	4.16	4.15	.93		1	.25	.25	6.44	*
Treatment:Occasion	2	3.04	1.52	2.11		2	.96	.48	1.35		2	35.00	17.4	3.92	*	2	1.25	.62	15.71	***
Residuals	240	172.76	.71			240	85.59	.35			240	1050.9	45.4			240	9.43	.03		

****p <0.001, **p <0.01, *p <0.05*, Blanks = *p >0.05*.

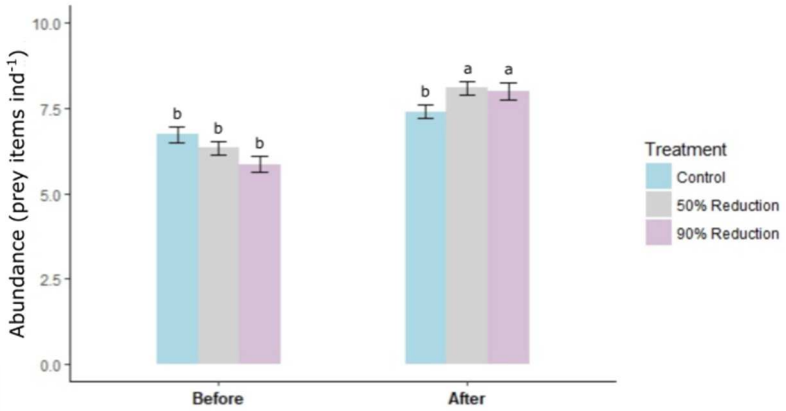

Figure 3.2: Lasting effect of experimental discharge reduction treatments on mean (± standard error) abundance of prey in the guts of salmon. Results of Tukey's post hoc comparisons shown: mean values sharing the same letter are not significantly different.

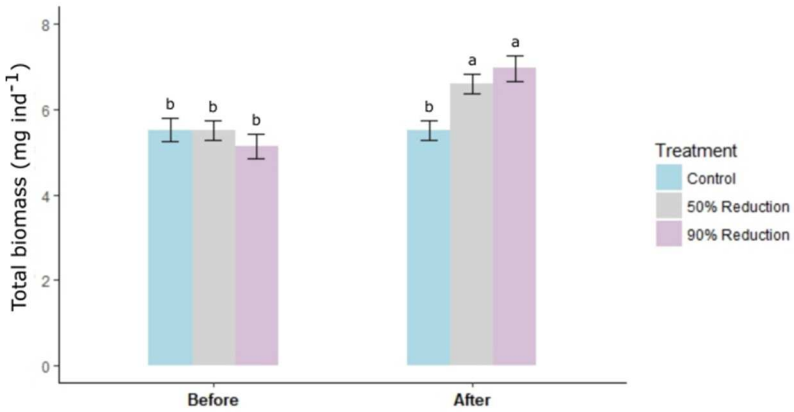

Figure 3.3: Lasting effect of experimental discharge reduction treatments on mean (± standard error) total biomass of prey in the guts of salmon. Results of Tukey's post hoc comparisons shown: mean values sharing the same letter are not significantly different.

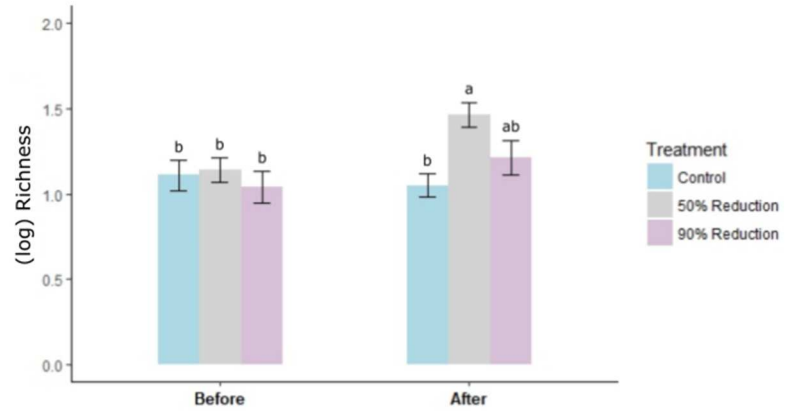

Figure 3.4: Lasting effect of experimental discharge reduction treatments on mean (± standard error) richness of prey items in the guts of salmon. Results of Tukey's post hoc comparisons shown: mean values sharing the same letter are not significantly different.

Table 3.3: Statistical results of the experimental effects (Treatment:Occasion) of reduced discharge on the abundance of individual taxa in the diet of salmonids tested using mvabund and calculated mean abundance (± variation) of those significant taxa. Abbreviations: Con/B: Control Before, Con/D: Control During, Con/A: Control After. 50/B: 50% reduction Before, 50/D: 50% reduction During, 50/A: 50% reduction After. 90/B: 90% reduction Before, 90/D: 90% reduction During, 90/A: 90% reduction After.

	Dev.	*P*	Con/B	Con/D	Con/A	50/B	50/D	50/A	90/B	90/D	90/A
Salmon											
Simuliidae lv.	240.89	***	4.38 (±10.08)	3.83 (±11.36)	9.19 (±20.03)	1.4 (±1.99)	2.05 (±3.37)	10.96 (±19.68)	1.86 (±5.06)	.04 (±0.19)	12.29 (±28.71)
0+ trout											
Gammarus pulex.	61.9	**	1.66 (±3.08)	.48 (±.87)	2.14 (±2.91)	1.56 (±2.50)	1.50 (±2.06)	2.22 (±3.50)	.95 (±1.48)	1.73 (±2.17)	1.58 (±2.04)
Simuliidae lv.	267.05	***	4.22 (±16.46)	5.63 (±16.43)	5.64 (±16.07)	1.96 (±2.39)	1.3 (±2.27)	3.78 (±6.67)	3.03 (±6.79)	.16 (±.42)	4.91 (±7.33)
1+ trout											
Gammarus pulex.	133.72	***	1.53 (±2.69)	1.06 (±1.67)	2.49 (±6.48)	3.39 (±6.84)	2.09 (±2.90)	2.73 (±8.89)	2.21 (±9.74)	4.45 (±9.74)	1.81 (±3.11)
Simuliidae lv.	485.47	***	4.51 (±17.09)	1.95 (±4.11)	1.57 (±3.47)	1.56 (±3.47)	.58 (±1.81)	1.11 (±2.44)	4.2 (±16.24)	.12 (±.37)	1.17 (±1.64)
≥2+ trout											
Baetidae lv.	43.26	*	1.04 (±2.30)	1.06 (±2.28)	1.09 (±2.27)	.98 (±2.10)	1.06 (±2.16)	.90 (±2.04)	.81 (±2.28)	.84 (±2.22)	.85 (±2.18)
Ephemerellidae lv.	38.47	*	.34 (±.91)	.33 (±.89)	.32 (±.87)	.30 (±.84)	.23 (±.76)	.27 (±.81)	.32 (±.86)	.30 (±.84)	.28 (±.82)
Gammarus pulex	101.85	**	1.85 (±4.24)	1.81 (±4.12)	1.76 (±4.04)	1.96 (±4.56)	1.42 (±3.92)	1.82 (±4.38)	2.44 (±5.34)	2.23 (±5.07)	2.17 (±4.94)
Gastropod	47.23	*	.81 (±3.06)	.95 (±3.11)	1.34 (±4.41)	1.23 (±4.11)	2 (±5.01)	1.30 (±3.99)	.76 (±3.17)	.80 (±3.10)	.76 (±3.02)
Limnephilidae lv.	36.97	*	.41 (±.98)	.46 (±1.04)	.53 (±1.18)	.64 (±1.34)	.79 (±1.43)	.62 (±1.31)	.45 (±1.13)	.45 (±1.12)	.43 (±1.02)
Nabidae	37.94	*	.02 (±.23)	.09 (±.52)	.10 (±.52)	.09 (±.50)	.55 (±1.92)	.33 (±1.51)	.04 (±.07)	.04 (±.06)	.04 (±.06)
Simuliidae lv	103.97	*	1.41 (±4.69)	1.37 (±4.57)	1.44 (±4.49)	1.73 (±10.04)	1.31 (±4.86)	1.61 (±9.59)	1.77 (±11.54)	1.67 (±11.21)	1.58 (±10.92)

****p <0.001, **p <0.01, *p <0.05*, Blanks = *p >0.05.*

Table 3.4: Statistical results of ANOVA testing the effects of a) reduced discharge and b) lasting effects of reduced discharge on the consumption rate of salmonids.

	a) Effects of reduced discharge										b) Lasting effects									
	Consumption rate (ind day^{-1})					Consumption rate (mg day^{-1})					Consumption rate (ind day^{-1})					Consumption rate (mg day^{-1})				
Source	**df**	**ss**	**ms**	**F**	***p***	**df**	**ss**	**ms**	**F**	***p***	**df**	**ss**	**ms**	**F**	***p***	**df**	**ss**	**ms**	**F**	***p***
Salmon																				
Year	2	4.162	2.08	3.07	*	2	24.89	12.44	5.4	**	2	3.67	1.83	2.69		2	13.69	6.84	4.01	*
Treatment	2	1.66	.83	1.23		2	4.72	2.35	1.02		2	2.53	1.26	1.86		2	15.11	7.55	4.43	*
Occasion	1	4.92	4.92	7.27	**	1	18.04	18.06	7.82	**	1	5.24	5.24	7.70	**	1	.03	.02	.01	
Treatment:Occasion	2	2.48	1.24	1.83		2	.2	.1	.04		2	2.92	1.46	2.14		2	10.88	3.44	2.19	
Residuals	243	164.34	.67			243	559.86	2.3			272	185.14	.68			272	463.22	1.7		
0+ trout																				
Year	2	12.72	7.86	12.38	***	2	9.78	4.89	2.32		2	16.29	8.14	12.73	***	2	43.33	21.66	11.41	***
Treatment	2	3.35	1.67	2.64		2	4.28	2.14	1.01		2	3.78	1.89	2.95		2	24.44	12.21	6.43	**
Occasion	1	3.74	3.74	5.89	*	1	2.95	2.95	1.40		1	1.19	1.18	1.85		1	3.46	3.46	1.82	
Treatment:Occasion	2	.55	.27	.43		2	40.12	20.05	9.54	***	2	1.82	.63	.99		2	.19	.09	.05	
Residuals	498	316.12	.63			498	1046	2.1			507	324.22	.63			507	962.22	1.89		
1+ trout																				
Year	2	5.01	2.5	3.61	*	2	18.30	9.15	2.29		2	.51	.25	.36		2	7.69	3.84	1.07	
Treatment	2	5.36	2.68	3.87	*	2	13.21	6.6	1.65		2	4.94	2.47	3.52	*	2	20.15	10.07	2.8	
Occasion	1	6.09	3.04	4.39	*	1	21.28	21.27	5.33	*	1	18.8	18.8	26.8	***	1	36.56	36.56	10.17	**
Treatment:Occasion	2	1.93	1.93	2.79		2	1.67	.83	.2		2	6.82	3.4	4.86	**	2	.59	.29	.08	
Residuals	454	314.61	.69			454	1809	3.98			469	328.9	.7			469	1685	3.59		
≥2+ trout																				
Year	2	.99	.49	.75		2	22.21	11.1	2.11		2	1.68	.83	1.32		2	36.4	18.2	4.16	*
Treatment	2	3.48	1.74	2.65		2	31.89	15.94	3.03		2	6.06	3.03	4.77	**	2	16.95	8.47	1.94	
Occasion	1	.38	.38	.58		1	1309	13.09	2.49		1	.23	.23	.37		1	5.26	5.29	1.21	
Treatment:Occasion	2	3.8	1.89	2.89		2	1.66	.83	.15		2	.8	.4	.63		2	20.11	10.05	2.3	
Residuals	220	144.35	.65			220	1155				236	150.01	.63			236	1030	4.36		

****p <0.001, **p <0.01, *p <0.05*, Blanks = *p >0.05*.

3.3.2 0+ trout

Effects of experimental discharge reduction treatments

The experimental reduction of discharge resulted in a significant difference in total biomass of prey in the guts of 0+ trout (Table 3.1), where total biomass was maintained between the Before and During occasions in the reduction treatments but declined significantly in the Control treatment (Figure 3.5).

Lasting experimental effects of the discharge reduction treatments resulted in a significant difference in the species richness of prey in the guts of 0+ trout (Table 3.2), where prey richness increased significantly between the Before and After occasions in the Control treatment, but not in the reduction treatments (Figure 3.6).

Abundance of individual prey taxa within the gut (Treatment:Occasion)

Mvabund analysis on the influence of the experimental design on prey consumed by 0+ trout identified significant effects for two taxa, *Gammarus pulex* and Simuliidae larvae (Table 3.3). For both Control and 50% reduction treatments, the mean abundance of *Gammarus pulex* in the guts of 0+ trout was lowest in the During occasion and highest in the After occasion, whereas in the 90% reduction treatment *Gammarus pulex* were more abundant in the During occasion and lowest in the Before occasion. Simuliidae larvae were less abundant in the guts of 0+ trout in the During occasion for both the 50% and 90% discharge reduction compared with the Control.

Consumption rate

There were no detectable effects of the experimental discharge reduction on the rate of consumption of individuals by 0+ trout (Table 3.4a). The experimental reduction of discharge resulted in a significant difference in the rate of consumption of biomass by 0+ trout (Table 3.4a), where consumption rate was significantly lower in the During occasion within the Control treatment compared with the Before (Figure 3.7). Overtime (Before–After) there was no change the rate of consumption of individuals and biomass by 0+ trout (Table 3.4b).

Electivity of prey

Overall there was a greater relative abundance of terrestrial prey in the guts of 0+ trout than in the environment (Figure A2.12 & A2.13).

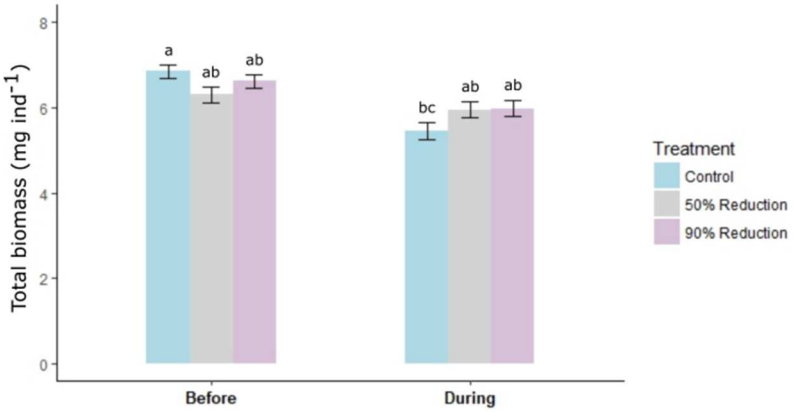

Figure 3.5: Influence of experimental discharge reduction treatments on mean (± standard error) total biomass of prey in the guts of 0+ trout (mg ind^{-1}). Results of Tukey's post hoc comparisons shown: mean values sharing the same letter are not significantly different.

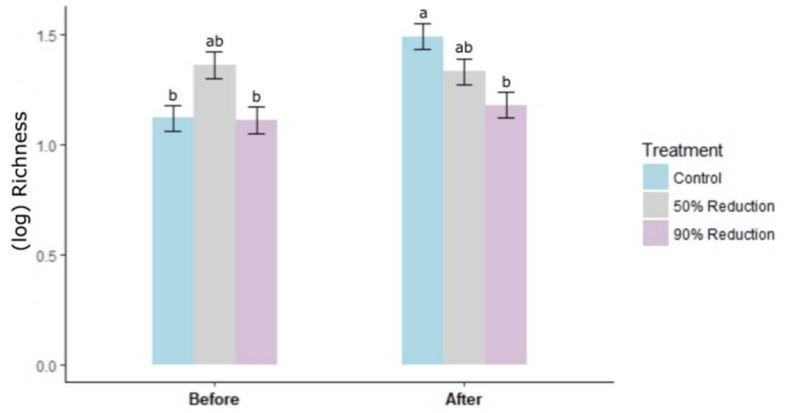

Figure 3.6: Lasting effect of experimental discharge reduction treatments on mean (± standard error) richness of prey types in the guts of 0+ trout. Results of Tukey's post hoc comparisons shown: mean values sharing the same letter are not significantly different.

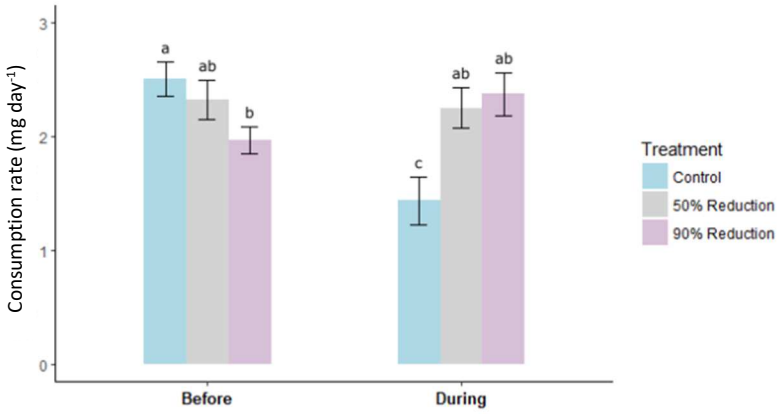

Figure 3.7: Influence of experimental discharge reduction treatments on mean (± standard error) consumption rate (mg day^{-1}) of 0+ trout. Results of Tukey's post hoc comparisons shown: mean values sharing the same letter are not significantly different.

3.3.3 1+ trout

Effects of experimental discharge reduction treatments

Significant experimental effect of reduced discharge was detected for richness, proportion of terrestrial biomass and abundance of prey in the guts of 1+ trout (Table 3.1). Species richness in the diet increased significantly between the Before and During occasions in the Control treatment, compared with the 50% and 90% reduction treatments where no change was detected (Figure 3.8). The proportion of terrestrial biomass increased significantly in the Control and 50% reduction treatment, between the Before and During sampling occasions, but not the 90% reduction treatment (Figure 3.9). Although there was a significant effect of Treatment:Occasion on the abundance of prey in the guts of 1+ trout, Tukey's post hoc test was unable to identify where these significant differences occurred (Figure 3.10). However, although not identified as significantly different by Tukey's test, the abundance of prey in the guts of 1+ trout decreased between the Before and During sampling occasions in the reduction treatments and increased in the Control. For all measures of gut contents, there were no detectable lasting effects of discharge reduction on 1+ trout (Table 3.2).

Abundance of individual prey taxa within the gut (Treatment:Occasion)

Similar to 0+ trout, mvabund analysis detected a significant effect of the experimental design on the abundance of *Gammarus pulex* and Simuliidae larvae in 1+ trout (Table 3.3). A 90% discharge reduction resulted in a higher mean abundance of *Gammarus pulex* in the guts of 1+ trout compared with the Control and 50% reduction treatments, where mean abundance decreased between the Before and During occasions. After the 90% reduction, the abundance of *Gammarus pulex* in the guts of 1+ trout decreased, whereas within the Control and 50% reduction treatments the abundance increased. There were fewer Simuliidae larvae in the guts of 1+ trout experiencing both the 50% and 90% reduction in discharge compared with the Control. However, the abundance of Simuliidae larvae in the guts of 1+ trout increased after flow had been reinstated in the 50% and 90% discharge reduction compared with the Control.

Consumption rate

There were no detectable effects of the experimental discharge reduction on the rate of consumption of individuals and biomass by 1+ trout (Table 3.4a). Lasting experimental effects of the discharge reduction treatments resulted in a significant difference in the consumption rate of 1+ trout, calculated as number of individual prey items (Table 3.4b). The rate of consumption of individual prey items decreased significantly between the Before and After occasions within both reduction treatments, but not in the Control treatment (Figure 3.11). There were no detectable lasting experimental effects of discharge reduction on the consumption rate of biomass of 1+ trout (Table 3.4b).

Electivity of prey

There was evidence of an increase in the electivity of *Gammarus pulex* from the drift by 1+ trout During 50% and 90% reduction treatments compared with the Control (Figure A2.14).

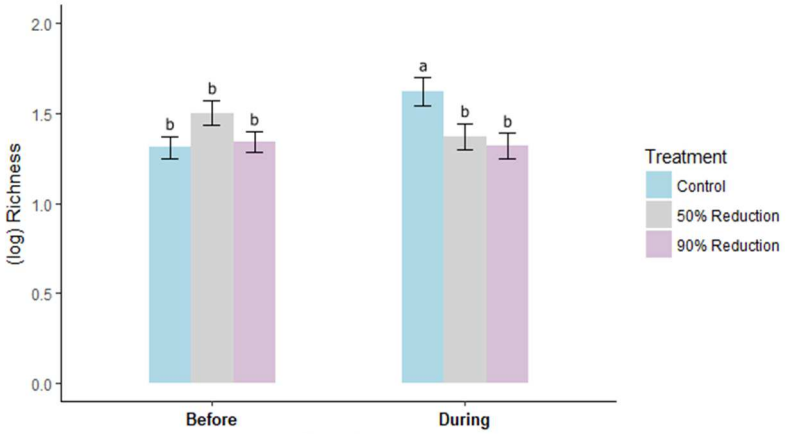

Figure 3.8: Influence of experimental discharge reduction treatments on mean (± standard error) richness of prey types in the guts of 1+ trout. Results of Tukey's post hoc comparisons shown: mean values sharing the same letter are not significantly different.

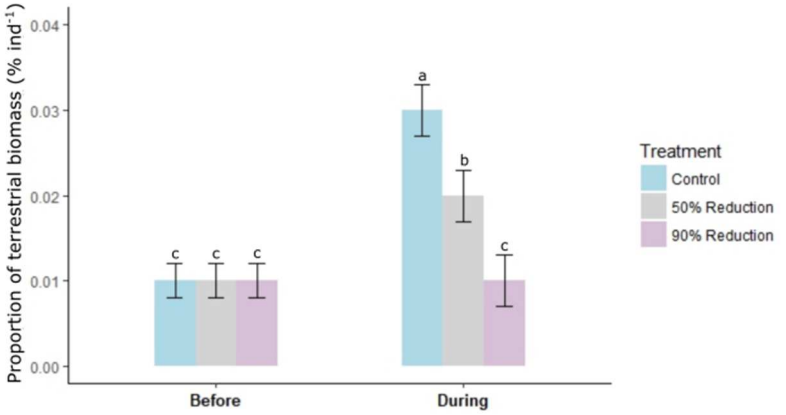

Figure 3.9: Influence of experimental discharge reduction treatments on mean (± standard error) proportion of terrestrial biomass (arc sin transformed) in the guts of 1+ trout. Results of Tukey's post hoc comparisons shown: mean values sharing the same letter are not significantly different.

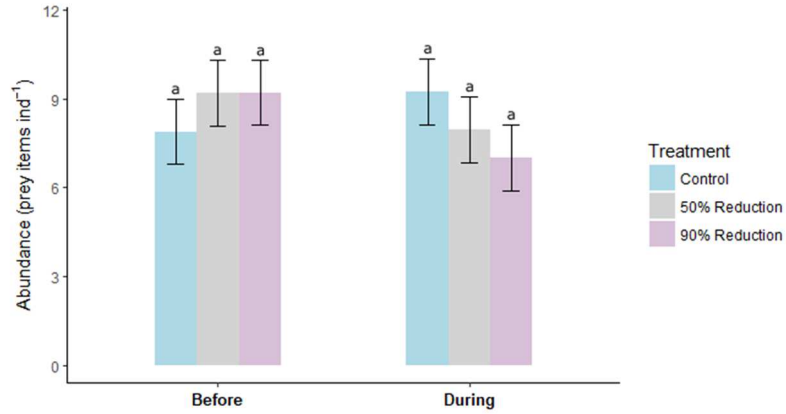

Figure 3.10: Influence of experimental discharge reduction treatments on mean (± standard error) abundance of prey in the guts of 1+ trout. Results of Tukey's post hoc comparisons shown: mean values sharing the same letter are not significantly different.

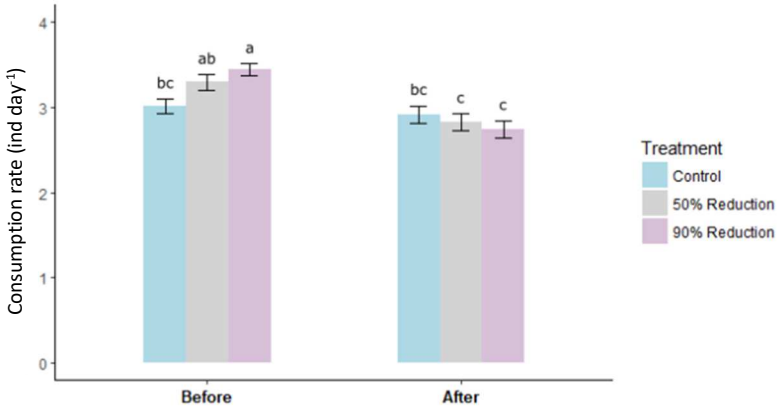

Figure 3.11: Lasting effect of experimental discharge reduction treatments on mean (± standard error) consumption rate (ind day^{-1}) of 1+ trout. Results of Tukey's post hoc comparisons shown: mean values sharing the same letter are not significantly different.

3.3.4 ≥2+ trout

Effects of experimental discharge reduction treatments

Similar to salmon, there was no detectable experimental effect of reduced discharge on the richness, abundance or measures of biomass consumed by ≥2+ trout (Table 3.1).

There was a detectable lasting experimental effect of discharge reduction on the proportion of terrestrial biomass in the guts of ≥2+ trout (Table 3.2): the proportion of terrestrial biomass was significantly lower than the Before occasion in ≥2+ trout that had experienced the 90% reduction treatment, compared with those from the Control and 50% reduction treatments (Figure 3.12). Although there was a significant effect of the Treatment:Occasion interaction on total prey biomass, Tukey's post hoc test was unable to identify where these significant differences were (Figure A2.15).

Abundance of individual prey taxa within the gut (Treatment:Occasion)

Mvabund analysis on the influence of the experimental design on the abundance of prey in the guts of ≥2+ trout identified significant effects for seven taxa (Table 3.3), including two families of mayflies (Baetidae larvae and Ephemerellidae larvae). Over time, within the Control and 90% reduction treatments, the mean abundance of Baetidae larvae in the diet increased, whereas the mean abundance of

Ephemerellidae larvae decreased. After the 50% reduction in discharge the abundance of Baetidae larvae in the diet decreased whereas the abundance of Ephemerellidae larvae increased compared to During.

Consumption rate

There were no detectable effects of the experimental discharge reduction, or any lasting effects, on the rate of consumption of individuals and biomass by ≥2+ trout (Table 3.4).

Electivity of prey

There was evidence that ≥2+ trout preferentially fed on larger prey items, such as Limnephilidae larvae and fish (Figure A2.16 & A2.17). Electivity for fish, i.e. piscivory, relative to the abundance available within the environment (Surber and drift) increased After the 50% reduction and During the 90% discharge reduction, compared with the Control.

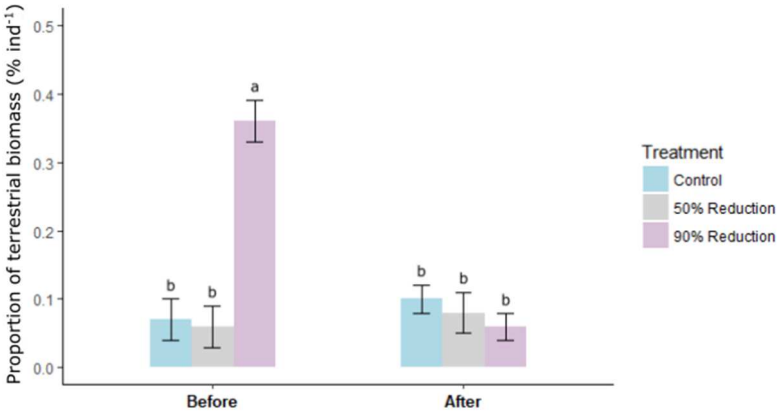

Figure 3.12: Lasting effect of experimental discharge reduction treatments on mean (± standard error) proportion of terrestrial biomass (arc sin transformed) in the guts of ≥2+ trout. Results of Tukey's post hoc comparisons shown: mean values sharing the same letter are not significantly different.

3.4 Discussion

The results of this study suggest that only certain aspects of salmonid diet were influenced by the experimental discharge reductions and it may be that plasticity in diet choice, and/or micro-habitat use, by salmonids allows for consumption rates to be maintained during reduced discharge.

Prey supply generally dictates the content of salmonid guts (Leung *et al*., 2009). Within this study the abundance and biomass of benthic macroinvertebrates (see section 2.3.3) and availability of drifting prey were not significantly affected by the experimental manipulation. These findings are contrary to Bunn & Arthington (2002) who suggested that benthic macroinvertebrates were vulnerable to rapid changes in discharge, and Minshall & Winger (1986) and González *et al*. (2018) who reported that reduced discharge lowered the rate of aquatic and terrestrial drift. However, these studies were not in chalk streams. In the current investigation, it is possible that no detectable difference in prey delivery rate between treatments were observed as the majority of aquatic drift in chalk streams occurs close to the stream bed (Neale *et al*., 2008). On the other hand, the lack of detectable effects of reduced discharge on invertebrate delivery rate may be attributable to the variation in delivery between replicates. Delivery rate of prey exhibits high spatial variation, and it is possible that increased spatial replication may have enabled a discernible relationship to be detected (Neale *et al*., 2008). As there were no detectible changes in prey availability throughout the experimental period, it is likely that any changes in gut content were a consequence of changes in the choice/preference of prey by salmon and trout. It is also possible that changes in diet may reflect any changes in the micro-habitats which the fish occupied (Mann *et al*., 1989).

Despite the limited numbers of salmon available in this study, salmon diet was influenced to a greater extent by the reinstatement of discharge to pre-manipulation levels than when discharge was reduced. The abundance, richness and biomass of prey in salmon guts increased following reinstatement of discharge, suggesting that salmon parr ate more prey, particularly more small prey, following the reinstatement of discharge compared with fish in the control treatment. It is possible that salmon parr increased their food intake to compensate for a preceding period of decreased habitat

availability, that may have caused an increase in the amount of time fish spent defending territories, due to increased fish density (Warren *et al*., 2015).

Salmon parr are reported to have a very narrow diet range that consists mainly of Simullidae, Batidae and Chironomidae (Bolnick *et al*., 2003; Sánchez-Hernández & Cobo, 2012). The diet range of salmon parr in this study was larger than previously reported and included preferential consumption of terrestrial prey. In these chalk streams, macrophytes may have made surface feeding more accessible by enabling salmon parr to seek terrestrial prey items in relative safety at the stream surface by providing adequate shelter, compared with other stream types. Despite the larger range of diet, this study found that, overall, Simulidae occurred in high abundances in the diet of salmon parr. Chalk stream substrate is typically fine and homogenous (Riley *et al*., 2006; Riley *et al*., 2009a), but during the summer, they are dominated by macrophytes, typically *Ranunculus penicillatus* subsp. *pseudofluitans* (Syme) S.D. Webster, which creates the instream architecture (creating refuge and velocity variations). Parr often use macrophytes as both shelter and feeding grounds (Riley *et al.,* 2006; Riley *et al.,* 2009b; House *et al*., 2017). As Simuliidae are typically found in high abundances on macrophytes (Gries & Juanes, 1998), they perhaps remained easier prey than other species.

Contrary to Gries & Juanes (1998), who reported that under reduced discharge salmonids abandon all types of foraging, discharge reduction in this study resulted in the maintenance of total gut biomass of 0+ trout and consumption rate remained high compared with the control treatment. Fornaroli *et al*. (2016) reported that reduced discharge can create favourable conditions for trout, which may have enabled 0+ trout to forage upon a larger area of the stream bed. Within spate rivers younger trout tend to be found predominantly in the margins, behind rocks or in back waters where there is potential refuge and the water velocity is favourable compared with mid-channel (Hubert *et al*., 1994; Roussel & Bardonnet, 1999; Johnson & McKenna, 2015). Although discharge reduction did not affect macrophyte abundance in the study streams (J.E.Marsh, unpubl. data), macrophytes would have occupied a greater proportion of the stream due to the decrease in water depth and wetted width (see section 2.3.1; Franklin *et al*., 2008). Such increases in cover/shelter may have enabled 0+ trout to

expend more energy on foraging rather than predator avoidance and maintenance of stream position. Reduced available habitat, under reduced discharge conditions, may have also resulted in larger prey items becoming more accessible enabling 0+ trout consumption rate of biomass to be maintained (Caldwell *et al*., 2018).

Reduced wetted area and increased movement between habitats can make smaller fish more vulnerable to predation during and after discharge reductions (Post & Parkinson, 2001; Lindeman *et al*., 2015). In this study piscivory increased in ≥2+ trout after the 50% discharge reduction and during the most severe (90%) reduction of discharge. Despite this increase in piscivory, there was no significant effect on the estimated size of the populations of younger salmonids (Chapter 5). Whilst cannibalism was detected, it is possible that older trout were eating mainly other fish species such as minnows (*Phoxinus phoxinus* (Linnaeus, 1758)), bullheads (*Cottus gobio* (Linnaeus, 1758)), stone loach (*Barbatula barbatula* (Linnaeus, 1758)) and sticklebacks (*Gasterosteidae* (Linnaeus, 1758)), which are also present in large numbers within the study streams (Riley *et al*., 2009a).

During the most severe discharge reduction, the mean abundance of *Gammarus pulex* in the diet of 1+ trout was higher than all other treatments within the During occasion. Ivlev's electivity index suggested that the higher abundance of *G. pulex* in the diet may have been due to an increased electivity of *G. pulex* from the drift. Neale *et al*. (2008) report that, within chalk streams, crustacea drift density is greatest during dusk and closer to the stream bed, which would have resulted in *Gammarus* being an easy prey target. Even though Ivlev's electivity index provides no tests of significance, it does suggest strength of selection or avoidance among possible prey: further tests would be necessary to determine the reasons why specific patterns in prey selection or avoidance were observed (Peckarsky, 2011).

Terrestrial prey usually constitutes a large proportion of the biomass in the guts of 1+ and ≥2+ trout (Dineen *et al*., 2007): in the current investigation 90% discharge reduction inhibited the natural increase of terrestrial biomass in the guts of 1+ trout, as detected within the control treatment. Perhaps, within the 90% reduction treatment, the reduction in wetted width reduced terrestrial in fall from bank side vegetation, resulting in less terrestrial prey being available.

Following the reinstatement of discharge, 1+ trout consumed fewer individuals of greater biomass compared to the control treatment. This lasting influence of reduced discharge maybe attributable to the change in feeding behaviour during reduced discharge conditions. Where discharge reduction reduced the abundance of prey in 1+ trout guts but had no effect on prey richness and total gut biomass remained unaltered throughout the experiment, suggesting that during discharge reduction 1+ trout had fewer larger individuals within their guts.

One of the benefits of this study was the ability to look for differences between streams and to see if any of the differences detected were attributable to the physical characteristics of each stream, which could be used to help guide any future management. Even though logical significant Treatment:Occasion were detected, stream findings of this study are consistent with French *et al*. (2016), who reported that salmonid diet was highly variable between streams. As no consistent Treatment:Occasion:Stream patterns were detected for each species/cohort it was not possible to assign the differences to stream physical attributes. For example, it is likely that salmon gut prey abundance increased over time (Before - After) in Fallodon when it was assigned a 90% reduction treatment, Blackbridge when it was a Control treatment and Brandy when it was a 50% reduction treatment, because of year effects (see Table 1.2 for assignment of discharge treatments between years). Salmonids are opportunistic foragers and the increase in the abundance of prey within the gut over time is likely to be in response to background environmental conditions for that year (Sánchez-Hernández & Cobo, 2012).

Overall, salmonids within these chalk streams displayed a high level of plasticity and ability to adapt to short term reductions in summer discharge. Dietary plasticity will increase a populations chance of remaining in their chosen habitat (Agrawal, 2001), but the extent to which growth rates and overall population condition can be maintained is unknown. As the level of plasticity exerted by fish is dependent upon stream characteristics (Musseau *et al*., 2015), chalk stream macrophytes may be essential in providing adequate shelter and food resources under reduced discharge to allow salmonid populations to adapt to projected changes in summer discharge conditions.

3.5 Conclusion

Even though reduced discharge did not result in the expected changes in macroinvertebrate drift rate (hypothesis 1), aspects of the diets of salmonids, as determined by gut contents (abundance, richness, total biomass and proportion of terrestrial biomass), did differ as a result of the experimental design but were not dominated by prey from the benthos (hypothesis 2). Increased encounter rate between individual fish During and After reduced discharge are likely to have led to the increased piscivory detected in older salmonids (hypothesis 3), but overall there was a limited effect on consumption rates (hypothesis 4), and where differences in stream over time were apparent they were not explicable by differences in the extent of physical change (Hypothesis 5).

The findings of this chapter provide evidence that the diets of wild salmonids are characterised by a high level of plasticity. Compensatory feeding limited any effects of reduced discharge, such that any effects on consumption rate (individual and biomass) were marginal. Chalk stream fish exhibit high dietary resilience which suggests that, within these streams, growth rate may not be limited by diet.

Projected changes in summer precipitation patterns and water use will undoubtably affect river discharge. Management strategies that concentrate predominantly on the maintenance of habitats, via environmental discharge setting, may be enough to enable effective conservation of salmonids during short periods of reduced discharge in chalk streams, as prey availability and fish plasticity, at least in this experiment, remained sufficient to maintain feeding rates. However, care needs to be taken where densities of 0+ salmon are greater or reductions in summer discharge last longer than a month, as increased piscivory by older trout could negatively impact this cohort.

Chapter 4: Does summer discharge reduction alter small scale salmonid habitat use in chalk streams?

4.1 Introduction

The distribution of salmonids in rivers and streams is primarily a consequence of the variation in abiotic variables, where salmonids are known to select stream habitats with particular characteristics (Armstrong *et al*., 2003; Riley *et al*., 2006). Two of the primary habitat variables that are known to affect habitat selection are water depth (Kennedy & Strange, 1982; Heggenes, 2002) and water velocity (Heggenes & Dokk, 2001; Conallin *et al*., 2014), where trout are reported to occupy habitats containing deeper and slower flowing waters than those occupied by salmon parr (Heggenes, 1996).

Salmonids will also assess the level of cover, either riparian or instream vegetation, when selecting preferential habitats (Milner, 1982; Riley *et al*., 2009b; Vowles & Kemp, 2019), and choose positions that maximise access to food resources, while minimising energy expenditure (Hughes & Dill, 1990) and predation risk (Ayllón *et al*., 2009). Substrate is also an important habitat variable as juvenile salmonids will often use substrate as refuges (Gries & Juanes, 1998). However, it has been reported that substrate is less critical for the juvenile life stage than for others, such as spawning (Hughes, 1992; Metcalfe *et al*., 1997; Greenberg & Giller, 2001). Salmonids are exothermic, therefore, water temperature will influence behaviour (Jonsson & Jonsson, 2009). Increases in water temperatures can affect habitat selection as salmonids seek thermal refuge and shelter (Gries & Juanes, 1998). Unlike spate streams, thermal buffering by groundwater contributions to discharge in chalk streams may dampen variations in water temperature (Chapter 2; Rolls *et al*., 2012), resulting in less marked changes in salmonid behaviour.

Diel patterns of light can influence habitat selection as the relative costs and benefits of activities may change (Gries *et al*., 1997; Metcalfe *et al*., 1998; Railsback *et al*., 2005). Imre & Boisclair (2004) reported that 0+ salmon were equally active in the day and at night, whereas older salmon were more active at night. Trout increase activity during crepuscular periods (dusk and dawn) as this is when prey availability is

the greatest (Ovidio *et al*., 2002). Others report that the habitats selected in the day and night are not substantially different (see Enders *et al*., 2009). Along with abiotic variables, competition between salmonid species/cohorts can influence the size of territories (areas) that are established (Keeley, 2000), and it is commonly accepted that bigger fish will be dominant and have larger (Keeley & Grant, 1995; Enders *et al*., 2009) or more optimal (Gowan & Fausch, 2002) areas than smaller individuals (Morrell & Kokko, 2003). However, it is possible that in the absence of such competition from bigger fish, smaller individuals may occupy more optimal habitat areas (Höjesjö *et al*., 2015).

Discharge reduction can cause widespread changes in the habitats available to salmonids, where water depth and the proportion of high velocity habitats are reduced (Gibson *et al*., 2005; Warren *et al*., 2015). Dependent upon channel form, lower water depths can reduce wetted width, thus, lateral connectivity between the stream channel and the established riparian zone are lost (Boulton, 2003; Lake, 2003). Severe discharge reductions can cause a break in hydraulic longitudinal connectivity as riffle habitats are lost and pools become the dominant flow type (Boulton, 2003; Lake, 2003).

There is some evidence that during moderate flow reduction the most beneficial response of salmonids is to adopt a 'sit it out' strategy (Armstrong *et al*., 1998; Riley *et al*., 2009a), as it may be better to continue to defend known habitats rather than move and compete for similar suboptimal habitat conditions elsewhere. During severe droughts salmon parr tend to move into deeper (pool) habitats (Verwey *et al*., 2018) but will periodically utilise riffle habitats occupied before drought conditions, if available (Armstrong *et al*., 1998), as a result of high site loyalty. However, it is not clear if salmon moved into pool habitats that are of similar absolute depths to what they occupied on riffle habitats before discharge decreased or, if they seek the deepest available water under discharge reduction.

Discharge reductions can also influence diurnal behaviour. Riley *et al*. (2009a) reported that under reduced discharge, on Brandy stream, salmon move into relatively deeper water during the day, possibly to reduce the risk of predation by avian predators (Reebs, 2002). However, movement into deeper water could increase

piscivory by older salmonids (Chapter 3) if encounter rates with older fish increase as, during discharge reduction, 1+ trout are reported to occupy relatively deeper and slower habitats during the day compared with faster flowing habitats at night (Riley *et al*., 2009a).

As a consequence of the reduction in available habitats, such as the elimination of established marginal habitats that are preferential to some juvenile salmonids (Koljonen *et al*., 2013), fish density will increase (Warren *et al*., 2015). At higher densities fish will be faced with greater levels of competition for prey and stream area, due to increased interaction (Stradmeyer *et al*., 2008; Nicola *et al*., 2015). If prey abundance is not limiting then it is likely that fish will remain within their original habitat but occupy smaller areas (Grant *et al*., 2017). However, competition for stream areas and predation pressure may increase if individuals occupy areas where they have to actively forage rather than preferentially drift feed (Martel, 1996; Kim *et al*., 2011; Sánchez-Hernández & Cobo, 2013).

The ability to move between and select different habitats is important for the survival for salmonids (Petty *et al*., 2012), particularly under reduced discharge conditions. But little is known what affects discharge reduction may have on habitat use once pre-reduction discharge has been reinstated. Both Armstrong *et al*. (1998) and Riley *et al*. (2009a) compared salmonid habitat use after discharge reinstatement to that of reduced discharge rather than pre-discharge reduction, where Armstrong *et al*. (1998) reported that salmon parr continued to use deep habitats once water flows are reinstated, indicating that drought has the potential to initiate redistribution within highly structured populations. In order to assess any lasting effects that discharge reduction may have on habitat use, comparison of before and after discharge reduction is paramount if management and conservation of freshwater fish are to evolve in response to present and the anticipated future conditions, and stream-scale experiments must take precedence to facilitate evidence-based management (Naiman & Latterell, 2005).

This chapter used portable PIT Multi-Point Decoder (hereafter MPD) systems (Riley *et al.,* 2003) to undertake an in-stream, field-based investigation into the response of salmon and trout in three chalk streams to two controlled, but

environmentally relevant, discharge reduction treatments. The aim was to determine whether discharge reduction altered small scale salmonid habitat use. Six hypotheses were tested: 1) the absolute depths and velocities that fish occupy decrease under reduced discharge conditions, 2) under reduced discharge conditions fish seek out relative depths and velocities that are greater to those occupied before reduced discharge conditions, 3) salmonid site loyalty will decrease under the most severe discharge reduction treatment, 4) the area used by fish will be smaller under reduced discharge conditions, and 5) reduced discharge will increase the differences in diel habitat use, home stone loyalty and area used. 6) Once discharge reduction has been reinstated, there will be lasting effects (Before-After) of reduced discharge on salmonid habitat use.

4.2 Methods

The study took place over three years. In each year, two of the three streams were subject to an experimental discharge reduction (50% or 90%). For information on the study sites and a detailed explanation of the discharge manipulations, see section 1.5.

4.2.1 Salmonid capture and PIT-tagging

Salmonids were captured using electrofishing three times every year (Before, During and After the experimental manipulation of discharge), for a detailed explanation of salmonid capture, see section 3.2.1. In addition, each MPD antennae array was fished separately to ensure the same fish were placed back over the antennas. Once captured and anesthetised, fish were scanned for the presence of a PIT tag (from previous surveys) and each year, during the Before fishing only, individuals without a tag had a PIT tag implanted. A needle was used to make an incision just anterior to the pelvic fins. A PIT tag (Wyre Micro Design Ltd.; 12 mm x 2.12 mm) was then inserted into the coelomic cavity (Riley *et al.,* 2003). The fish were then left to recover for c. 2 hours before being returned to the site of capture.

4.2.2 Salmonid location using PIT antenna systems

A portable PIT MPD system was installed at the same location in each stream over the three experimental years to detect the microhabitat used by individual PIT

tagged fish (Figure 4.1; Riley *et al*., 2003). The MPD system consisted of one 24 V DC integrated MPD/antenna multiplexer (16 channel), two 12 V gel lead-acid batteries, a Global Point System (GPS) device, 16 circular black panel antennae and a logger where data were stored on a removable memory card (Plate 4.1). The GPS device was used to correct any logger time (GMT) drift. The MPD/antenna multiplexer sequentially polls/ interrogates all 16 antennae every 3.2 s (read time of 200 ms per antenna). When a PIT tag is detected at an antenna, its unique ID code is saved to the logger, together with the antenna number and the detection date and time. Each circular panel antenna was 22 mm deep and 300 mm in diameter, including a 20 mm surrounding flange, and had a typical PIT tag detection range of c. 90 mm. This detection range is compatible with small scale salmonid habitat studies, as they are known to hold positions close to the stream bed and visual observations indicate this to be the case during directed movement (Armstrong *et al*., 1996).

The antennae were placed in three rows, two rows of five antennae and one row of six, where each row was 5 m apart from adjacent rows (see Figure 4.2). The first antenna in each row was positioned next to the true right-hand bank; subsequent antennae were placed 0.8 m apart (Plate 4.2; Figure 4.2). All antennae were dug into the surface of the stream bed; antennae and cables were secured in the stream using pegs. Once installed, PIT tags were used to assess antennae efficiency. Any antennae that were deemed to be either inefficient (i.e. tags were not detected within one cycle of the multiplexer) or not working, were replaced. Antenna efficiency was also tested at the end of each experimental year, in order to determine if any had a reduced efficiency or had failed all together.

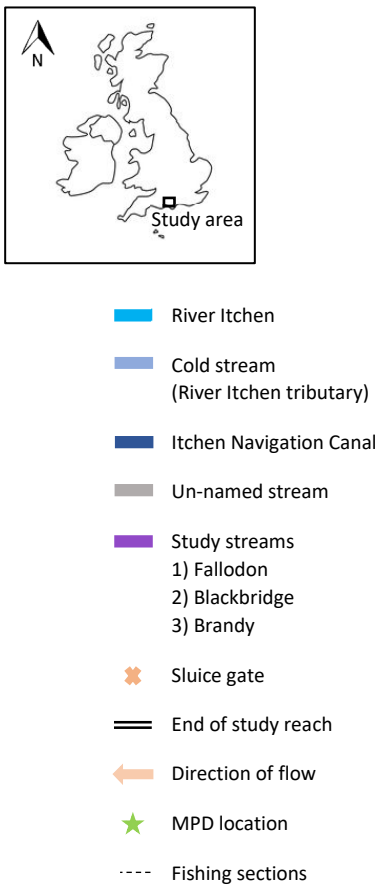

Figure 4.1: Map displaying the location of the different sites, extent of study streams and location of MPD systems and predefined electrofishing sections. OS maps accessed 27/02/2019.

Plate 4.1: Example layout of the MPD system including: multiplexer, data logger, batteries and GPS deployed at Fallodon Stream.

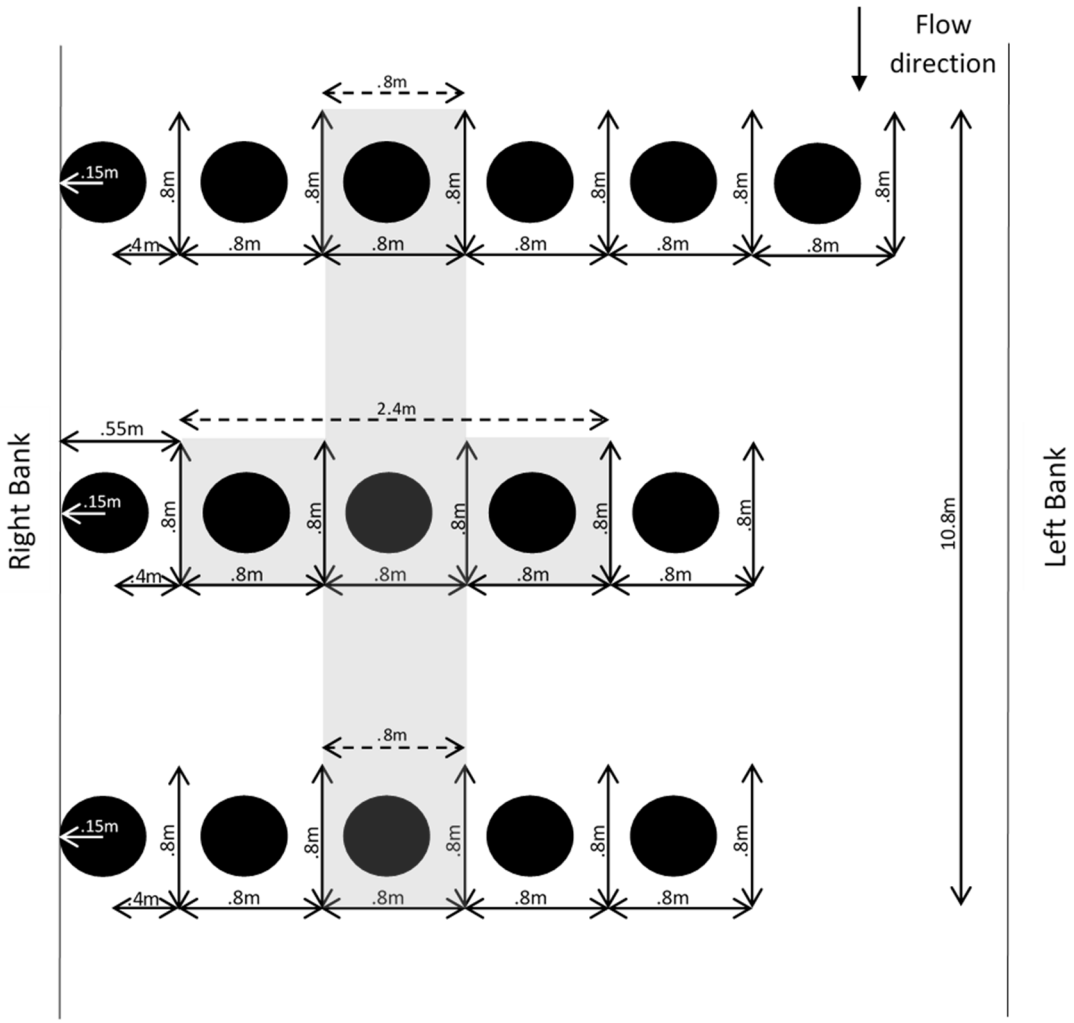

Figure 4.2: Graphical representation of the array of PIT antennae controlled by the multipoint decoder in each stream and the distance between each antenna. Area used (m2) = mean width covered * length of stream used. Note: not to scale. Black circles represent the antennae and grey boxes are the example detection areas.

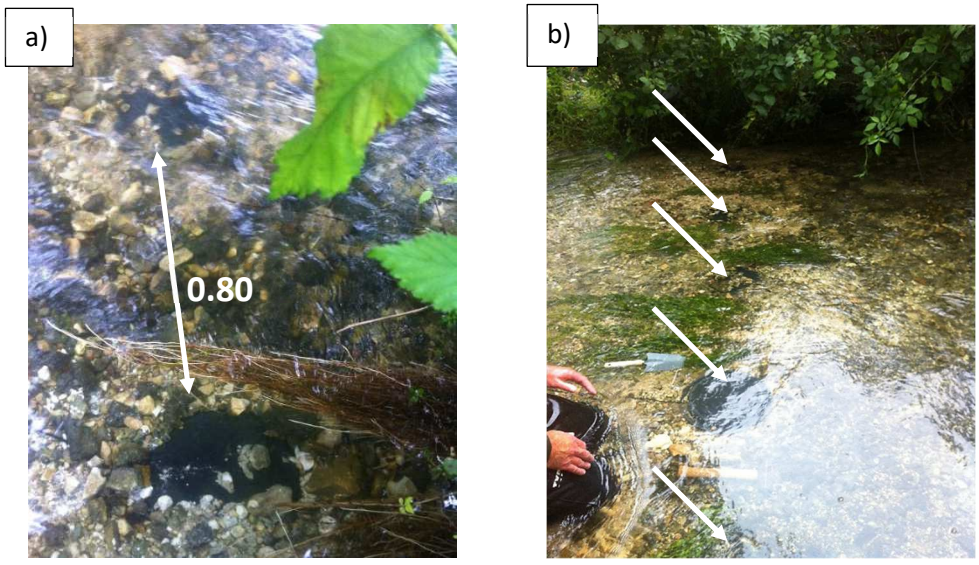

Plate 4.2: Location of the antennae within Fallodon stream. (a) antennae, 0.80 m apart, (b) complete line of antennae after installation (white arrows).

4.2.3 Habitat surveys

Details of the habitat at each individual PIT antenna were recorded during each of the experimental occasions (Before, During and After). Water depth was measured to the nearest 0.05 m. Mean velocity was determined (over 60 s) in mid-water using a Valeport 'Braystoke' BFM002 current flow meter (accuracy: ± 0.01 m s^{-1} below 0.5 m s^{-1}; ± 2.5% reading above 0.5 m s^{-1}; see Plate 2.1).

4.2.4 Data preparation

A total of 39 salmon (1,023,586 detections) and 427 trout (3,254,280 detections) PIT tags were detected and recorded during the three experimental years. Before data analysis, steps were taken to ensure data integrity between all years: 1) any tag codes that couldn't be assigned to fish (detection errors) and detections from faulty antennas with unknown efficiency or efficiency that changed over time were removed. 2) Individuals that were initially tagged in one stream but were subsequently caught/detected in another within a given year were removed. 3) The data were then trimmed into four equal detection periods, so each occasion had the same number of detection days (See Figure 4.3 & Table A3.1). 4) Due to a faulty MPD system in Fallodon stream, leading to only 5 hours of detections being recorded, within the Before detection period in 2015, all detections in this period were removed. 5) Individuals with only one observation per year were removed from the analysis because it would not be possible to determine if the habitat or area used by these individuals changed over time. This left 29 salmon (828,690 detections) and 337 trout (2,693,783 detections) for the analysis. Due to the small numbers of salmon detected 0+ and 1+ ages were grouped and trout aged 2+ or older were grouped into the ≥2+ category (see Table A3.2 for number of salmonids and detections after each data preparation step; see Table A3.3 for a breakdown of the final number of fish and detections).

Sunrise and sunset times for the study location were obtained from https://www.sunrise-and-sunset.com/en/sun/united-kingdom/winchester. The period between sunrise and sunset was designated as day, and periods of rapidly changing light before sunrise (dawn) and after sun set were incorporated into the night category (as per Riley *et al*., 2009a).

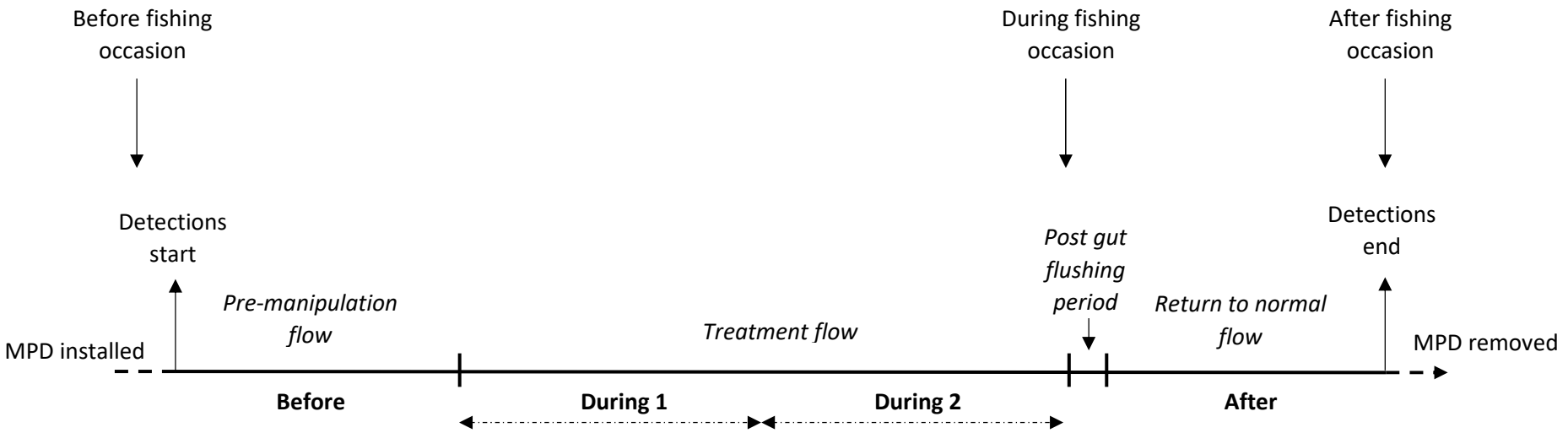

Figure 4.3: MPD experimental timeline followed over the three years with each stream experiencing their assigned treatment. Four distinct detection periods analysed in **bold.** Each detection period was 9 days long.

4.2.5 Statistical analysis

Habitat use

As each stream experienced all discharge treatments (Control, 50% and 90% reduction) over the three years (2015, 2016, 2017), a decision was required as to whether Stream or Year should be used within the analytical model as they both can influence differences within the fish community. In order to do this, fish densities in each stream in the Before detection periods were plotted to determine whether the densities of species/cohort, were similar/different between years and streams (Figure A3.1). Despite some variation between years, the differences in densities between streams were greater. The environment in each of these three streams is usually very stable due to the relatively constant discharge dictated by the sluice gates at the top of each stream. However, the individual streams did differ in depth, velocity and wetted width (see section 2.3.1) and there were differences in biological traits expressed by the fish among the streams, such as fish diet (see Chapter 3). Therefore, Stream was used as a spatial block within the analytical model.

When comparing habitat use across detection periods, changes in relative depths and velocities used were analysed in addition to absolute measurements, to determine if habitat use under reduced discharge conditions changed relative to the habitat available during a specific detection period; for example, if fish had moved to the deepest location available during discharge reduction. As discharge reduction rendered some antennae to become un-accessible by fish (e.g. an antenna is out of the water), for each detection period relative depth was defined as observed depth minus the mean depth of all the available antennae, and relative velocity as the observed velocity minus the mean velocity at all the available antennae.

To ensure that the results were not dominated by few fish with a high number of detections (Figure A3.2 - A3.7), habitat use was summarised by calculating the absolute and relative depth/velocity for each individual fish detection, then taking the mean for each individual across species, cohort, treatment, detection period and day/night. Analysis of habitat use was carried out separately for each species cohort

and analysed using `lmer` using the lme4 package with Tukey's post hoc tests in R-studio (R Core Team, 2018).

Site loyalty

In order to determine if the initial effects of discharge reduction (Before–During1&2) and any lasting effects (Before-After) resulted in the disruption to salmonid site loyalty, the antennae each tagged individual had been recorded on most often was determined (mode antenna). Mode antennae in the Before–During1&2 and Before–After detection periods were linked by PIT tag code so that only individuals that were detected in both periods were analysed. Each tag code was then scored 0 if mode antennae remained the same or 1 if it changed. The data were analysed using GLM with family = "bionomial" and Tukey's post hoc tests, to determine if the proportion of fish that stayed on the same antennae changed with Treatment and Treatment:DayNight. The analysis was carried out separately for each species/cohort combination.

Stream area used

Sequential recording of individual fish at the same or adjacent antennae during each detection period allowed the estimation of range of movement (used here as a proxy for stream area used). The width of river utilised was estimated as the product of the mean number of antennae detected on each line (the width of river allocated to each antenna in a line is 0.8 m). Antennae at the right-hand bank were allocated only 0.55 m of river width as they were placed against the bank. For example, if a fish was recorded at one antenna on the first line, three antennae on the second line and one on the third line, the mean width used across stream = (0.8 m + 2.4 m + 0.8 m) / 3 antennae lines (see Figure 4.2). If fish were detected on only one line of antennae, the length of the river used was 0.8 m (as such each individual antenna had an allocated detection area of 0.8 m x 0.8 m). If a fish was detected on two lines of antennae, 5 m was added to the length of stream used as the antennae lines are 5 m apart, and 10 m was added if a fish was detected on all three lines. Area used (m^2) of each fish was calculated as mean width covered * length of stream used. The data were analysed using `lmer` in lme4 package with Tukey's post hoc tests, to determine if stream area

used by fish decreased under reduced discharge conditions (Treatment:DetectionPeriod) and if there were differences in area used during the day and at night (Treatment:DetectionPeriod:DayNight). Stream area used was log transformed to avoid any negative fitted values. The analysis was carried out separately for each species/cohort combination.

In line with pervious chapters, the analyses investigated the effects of discharge reduction (Before–During1&2) and reinstatement (Before–After). All data preparation and analyses were undertaken in R-studio (R Core Team, 2018).

4.3 Results

4.3.1 Salmon

The experimental discharge reduction resulted in significant differences in the absolute water depth and velocity used by salmon over the detection periods (Table 4.1a). Within the During detection periods, salmon within the 90% discharge reduction treatment were located in significantly shallower and slower water compared with the Before detection period, whereas there was no change in the Control and 50% reduction treatments (Figure 4.4 & Figure 4.5). After discharge reinstatement, salmon in all treatments were in absolute water depths and velocities that were not significantly different to the Before detection period (Figure 4.4 & Figure 4.5).

Discharge reduction resulted in significant differences in the relative depth used by salmon (Table 4.1b). Although Tukey's post hoc test could not detect any differences ($p > 0.05$), the data suggests that, within both During occasions, salmon used relatively shallower water within the 90% reduction treatment compared with the Control and 50% discharge reduction (Figure 4.6).

There was a significant difference in site loyalty for salmon between the Before and During1&2 detection periods among treatments (Table 4.2a), where 93.3% of fish moved away from the mode antenna during a 90% discharge reduction compared with 25% in the Control (Table 4.3; Tukey's post hoc test $p < 0.05$). There were no lasting effects of experimental discharge reduction (Before-After) on site loyalty for salmon (Table 4.2b), and no detectable effects of discharge reduction on area used (Table 4.4).

Table 4.1: Statistical results of ANOVA testing discharge reduction treatments, detection periods and day/night effects on the a) absolute and b) relative depth/velocity used by salmonids. DetecPer = Detection period. Interactions of interest highlighted in **bold**.

	a) Absolute										b) Relative									
	Depth (cm)					Velocity (m s^{-1})					Depth					Velocity				
Source	df	ss	ms	F	*p*	df	ss	ms	F	*p*	df	ss	ms	F	*p*	df	ss	ms	F	*p*
Salmon																				
Stream	2	447.6	223.8	13.81	***	2	0.12	0.06	3.17		2	75.8	37.9	2.49		2	0.06	0.03	1.68	
Treatment	2	11.4	5.7	0.35		2	0.01	0.01	0.31		2	21.0	10.5	0.69		2	0.02	0.01	0.64	
DetecPer	3	242.3	80.7	4.98	**	3	0.58	0.19	9.52	***	3	77.9	25.9	1.71		3	0.17	0.05	2.91	*
DayNight	1	49.1	49.1	3.03		1	0.01	0.01	0.42		1	38.5	38.5	2.53		1	0.01	0.01	0.45	
Treatment:DetecPer	6	976.9	162.8	10.05	***	6	0.51	0.08	4.11	***	6	224.6	37.4	2.46	*	6	0.16	0.02	1.33	
Treatment:DetecPer:DayNight	11	195.6	17.7	1.09		11	0.18	0.01	0.84		11	192.4	17.4	1.14		11	0.18	0.01	0.81	
0+ trout																				
Stream	2	2415.4	1207.7	69.33	***	2	0.20	0.10	4.98	**	2	154.7	77.3	4.69	*	2	0.47	0.23	11.83	***
Treatment	2	167.1	83.54	4.79	**	2	0.31	0.15	7.44	***	2	19.2	9.6	0.58		2	0.11	0.05	2.65	
DetecPer	3	1153.5	384.5	22.07	***	3	1.45	0.48	23.71	***	3	88.1	29.3	1.78		3	0.17	0.06	2.93	*
DayNight	1	33.5	33.5	1.92		1	0.02	0.02	1.43		1	32.1	32.1	1.95		1	0.02	0.02	1.34	
Treatment:DetecPer	6	1231.8	205.3	11.78	***	6	0.74	0.12	6.04	***	6	245.8	40.9	2.48	*	6	0.11	0.01	0.93	
Treatment:DetecPer:DayNight	11	341.3	31.1	1.78		11	0.31	0.02	1.40		11	238.9	30.8	1.86		11	0.31	0.02	1.42	
1+ trout																				
Stream	2	725.2	362.6	30.91	***	2	0.97	0.48	24.08	***	2	81.1	40.5	3.84	*	2	0.36	0.181	9.40	***
Treatment	2	325.6	162.8	13.87	***	2	0.22	0.11	5.46	**	2	208.1	104	9.85	***	2	0.07	0.039	0.13	
DetecPer	3	1126.3	375.4	31.99	***	3	0.83	0.27	13.64	***	3	135.6	45.2	4.28	**	3	0.05	0.018	0.40	
DayNight	1	5.4	5.4	0.46		1	0.01	0.01	0.05		1	11.3	11.3	1.07		1	0.01	0.001	0.94	
Treatment:DetecPer	6	904.1	150.6	12.84	***	6	0.59	0.09	4.89	***	6	68.8	11.4	1.08		6	0.08	0.013	0.65	
Treatment:DetecPer:DayNight	11	61.2	5.57	0.47		11	0.08	0.01	0.37		11	64.3	5.8	0.55		11	0.08	0.007	0.96	
≥2+ trout																				
Stream	2	247.1	123.5	14.49	***	2	0.49	.024	22.62	***	2	22.1	11.1	1.47		2	0.11	0.05	5.22	**
Treatment	2	138.7	69.3	8.14	***	2	0.04	0.02	2.30		2	32.4	16.2	2.17		2	0.05	0.02	2.49	
DetecPer	3	515.1	171.7	20.16	***	3	0.02	0.01	0.64		3	185.4	61.8	8.27	***	3	0.06	0.02	1.97	
DayNight	1	2.5	2.52	0.29		1	0.01	0.01	1.53		1	4.4	4.4	0.59		1	0.02	0.02	2.20	
Treatment:DetecPer	6	437.2	72.8	8.55	***	6	0.36	0.06	5.63	***	6	97.1	16.1	2.16		6	0.33	0.05	5.34	***
Treatment:DetecPer:DayNight	11	71.7	6.52	0.76		11	0.63	0.05	5.32	***	11	73.8	6.7	0.89		11	0.64	0.05	5.60	***

****p <0.001, **p <0.01, *p <0.05*, Blanks = *p >0.05*.

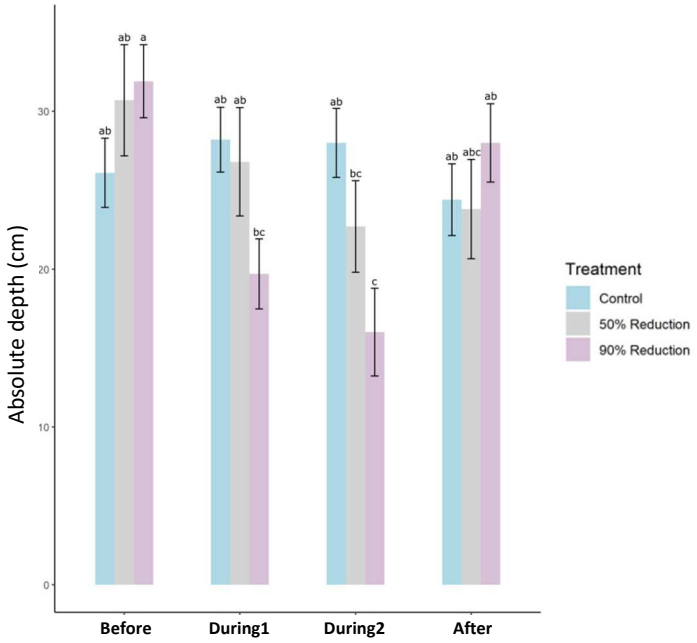

Figure 4.4: Influence of the experimental discharge reduction treatments on mean (± standard error) absolute depth (cm) used by salmon. Results of Tukey's post hoc comparisons shown: mean values sharing the same letter are not significantly different.

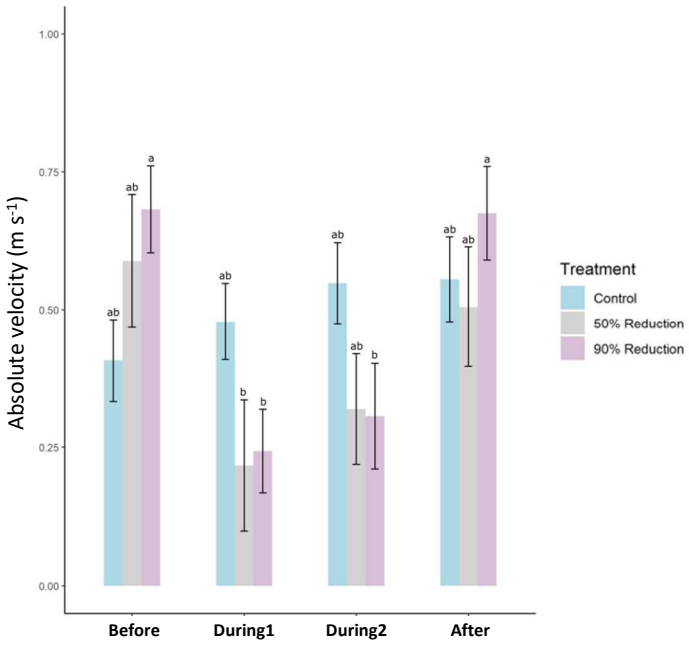

Figure 4.5: Influence of the experimental discharge reduction treatments on mean (± standard error) absolute velocity (m s^{-1}) used by salmon. Results of Tukey's post hoc comparisons shown: mean values sharing the same letter are not significantly different.

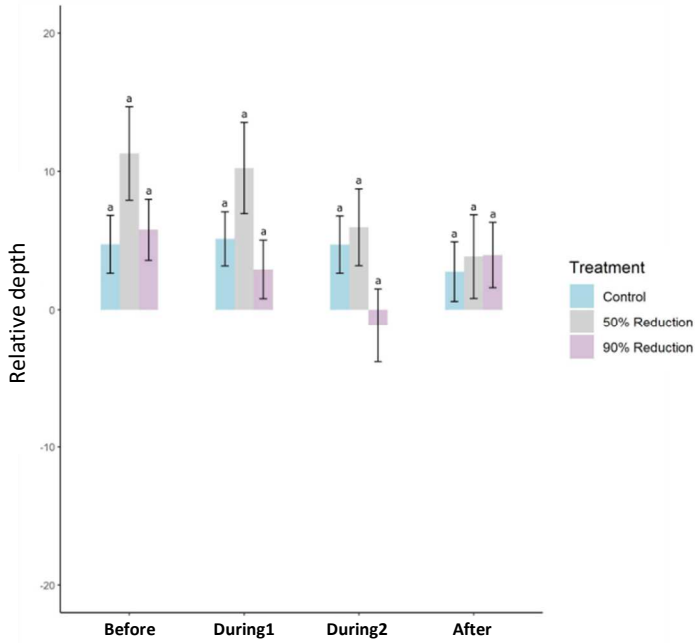

Figure 4.6: Influence of the experimental discharge reduction treatments on mean (± standard error) relative depth used by salmon. Results of Tukey's post hoc comparisons shown: mean values sharing the same letter are not significantly different.

Table 4.2: Analysis of deviance table for change in site loyalty used by salmonids in relation to the a) initial and b) lasting effects of discharge reduction. GLMs were fit separately for each species/age combination.

Source	a) Initial effects of reduced discharge						b) Lasting effects				
	Residual df	Residual deviance	df	Change in deviance	*p*		Residual df	Residual deviance	df	Change in deviance	*p*
Salmon											
Stream	20	20.45	2	11.38	**		11	14.22	2	0.31	
Treatment	18	16.86	2	3.59	*		9	11.59	2	2.63	
DayNight	17	15.81	1	1.04			8	6.59	1	5.01	*
Treatment:DayNight	15	15.34	2	0.46			6	6.98	2	0.71	
Error	22	31.84					13	14.54			
0+ trout											
Stream	122	170.31	2	1.17			99	131.62	2	1.99	
Treatment	120	163.71	2	6.59	*		97	130.37	2	1.25	
DayNight	119	162.91	1	0.79			96	130.37	1	0.01	
Treatment:DayNight	117	160.17	5	2.74			94	126.08	2	2.28	
Error	124	171.48					101	133.62			
1+ trout											
Stream	132	182.06	2	3.42			81	115.91	2	0.11	
Treatment	130	179.98	2	2.07			79	108.17	2	0.21	
DayNight	129	179.83	1	0.15			78	108.15	1	0.01	
Treatment:DayNight	127	179.78	5	0.04			76	107.17	2	0.98	
Error	134	185.48					83	116.02			
≥2+ trout											
Stream	38	52.33	2	1.51			22	29.24	2	2.09	
Treatment	36	40.91	2	11.43	**		20	29.19	2	0.04	
DayNight	35	40.71	1	0.19			19	19.17	1	0.02	
Treatment:DayNight	33	40.53	2	1.16			18	24.81	1	1.57	
Error	40	53.85					24	31.34			

****p <0.001, **p <0.01, *p <0.05*, Blanks = *p >0.05*.

Table 4.3: Observed number and (percentage) of fish that either remained at the same site or relocated to a different site between the Before and During1&2 detection periods across all discharge reduction treatments.

	Salmon		0+ trout		1+ Trout		≥2+ trout	
Treatment	Same	Different	Same	Different	Same	Different	Same	Different
Control	9 (75)	3 (25)	17 (65.4)	9 (34.6)	24 (57.1)	18 (42.9)	11 (57.9)	8 (42.1)
50% reduction	2 (100)		38 (62.3)	23 (37.7)	22 (39.3)	34 (60.7)	4 (30.8)	9 (69.2)
90% reduction	1 (6.7)	14 (93.3)	15 (39.5)	23 (60.5)	14 (37.8)	23 (62.2)	2 (18.2)	9 (81.9)

Table 4.4: Statistical results of ANOVA testing discharge reduction treatments, detection period and day/night effects on the stream area (m^2) used by salmonids. DetecPer = Detection period. Interactions of interest highlighted in **bold**.

	Area (m^2)				
Source	df	ss	ms	F	*P*
Salmon					
Stream	2	8.25	4.12	9.34	**
Treatment	2	3.44	1.72	3.90	*
DetecPer	3	1.43	0.47	1.08	
DayNight	1	0.01	0.1	0.02	
Treatment:DetecPer	6	5.68	0.94	2.14	
Treatment:DetecPer:DayNight	11	3.37	0.31	0.69	
0+ trout					
Stream	2	0.88	0.44	0.65	
Treatment	2	5.78	2.89	4.32	*
DetecPer	3	2.29	0.76	1.14	
DayNight	1	0.46	0.46	0.69	
Treatment:DetecPer	6	3.48	0.58	0.86	
Treatment:DetecPer:DayNight	11	27.12	2.46	3.68	***
1+ trout					
Stream	2	6.13	3.06	2.93	
Treatment	2	3.29	1.64	1.57	
DetecPer	3	10.81	3.60	3.43	*
DayNight	1	1.98	1.98	1.89	
Treatment:DetecPer	6	10.29	3.04	2.09	**
Treatment:DetecPer:DayNight	11	18.16	1.65	1.57	
≥2+ trout					
Stream	2	3.92	1.96	2.34	
Treatment	2	3.33	1.66	1.99	
DetecPer	3	0.33	0.11	0.13	
DayNight	1	4.23	4.23	5.07	*
Treatment:DetecPer	6	1.34	0.22	0.26	
Treatment:DetecPer:DayNight	11	6.98	0.63	0.76	

****p <0.001, **p <0.01, *p <0.05*, Blanks = *p >0.05*.

4.3.2 0+ trout

The experimental discharge reduction resulted in significant differences in the absolute water depth and velocity used by 0+ trout over the detection periods (Table 4.1a). Similar to salmon, within both During detection periods, 0+ trout within the 90% discharge reduction treatment utilised significantly shallower and slower water compared with the Before (Figure 4.7 & Figure 4.8). In addition, 0+ trout within the 50% reduction treatment utilised shallower absolute water depths compared with the Before (Figure 4.7). Following the reinstatement of discharge, 0+ trout that had experienced a 90% discharge reduction remained in shallower water depths compared with the Before detection period (Figure 4.7), whereas 0+ trout that had experienced a 50% reduction were located within faster water velocities compared with the Before detection period (Figure 4.8).

Discharge reduction resulted in significant differences in the relative water depth used by 0+ trout (Table 4.1b). In the initial stages (During1) of a 90% discharge reduction 0+ trout were found in relatively shallower water compared with the Before detection period (Figure 4.9). Discharge reinstatement resulted in no significant difference in relative water depth used by 0+ trout between the Before and After detection periods across all treatments (Figure 4.9).

There was a significant difference in site loyalty for 0+ trout between the Before and During detection periods among treatments (Table 4.2a), although the Tukey's post hoc test could not identify differences between the absolute values ($p > 0.05$). The percentages of fish that either remained at the same mode antennae or moved to a different mode antennae suggest that there was a reduction in the proportion of 0+ trout that remained at the mode antenna between the Before and During1&2 detection periods in the 90% discharge reduction treatment (39.5%) compared with the Control (65.4%; Table 4.3). There were no lasting effects of discharge reduction (Before-After) on site loyalty for 0+ trout (Table 4.2b).

Experimental discharge reduction resulted in differences in the area used by 0+ trout during the day compared with area used at night (Table 4.4). There was a significant increase in the area used by 0+ trout at night under a 90% discharge

reduction treatment in the During2 detection period compared with the day (Figure 4.10).

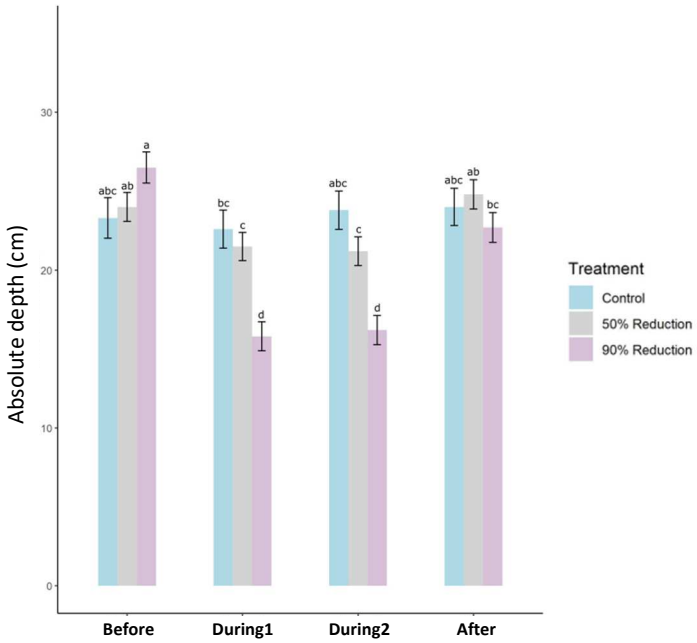

Figure 4.7: Influence of the experimental discharge reduction treatments on mean (± standard error) absolute depth (cm) used by 0+ trout. Results of Tukey's post hoc comparisons shown: mean values sharing the same letter are not significantly different.

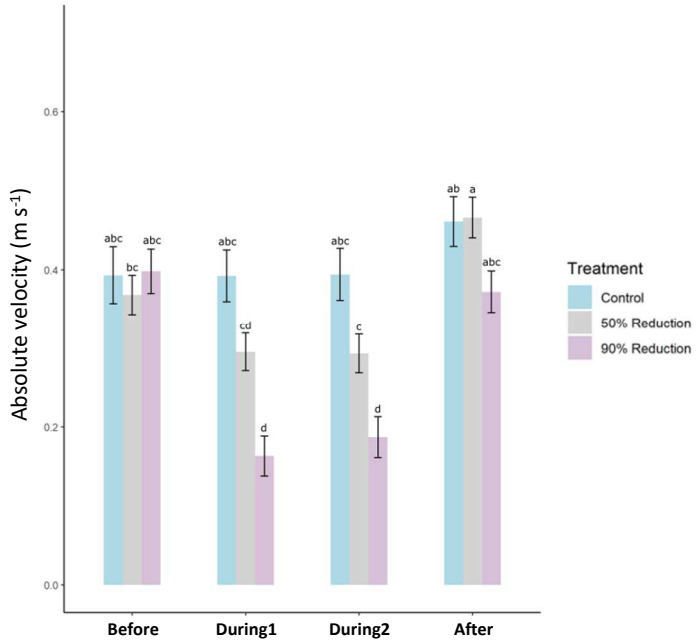

Figure 4.8: Influence of the experimental discharge reduction treatments on mean (± standard error) absolute velocity (m s^{-1}) used by 0+ trout. Results of Tukey's post hoc comparisons shown: mean values sharing the same letter are not significantly different.

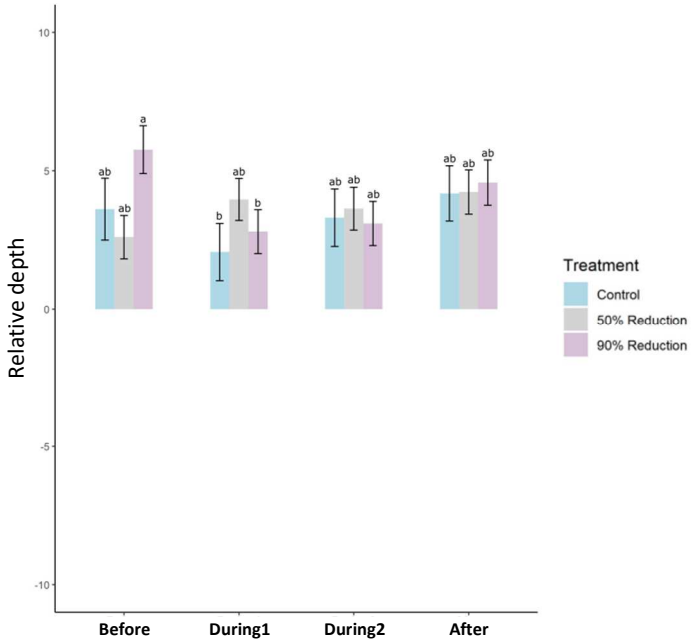

Figure 4.9: Influence of the experimental discharge reduction treatments on mean (± standard error) relative depth used by 0+ trout. Results of Tukey's post hoc comparisons shown: mean values sharing the same letter are not significantly different.

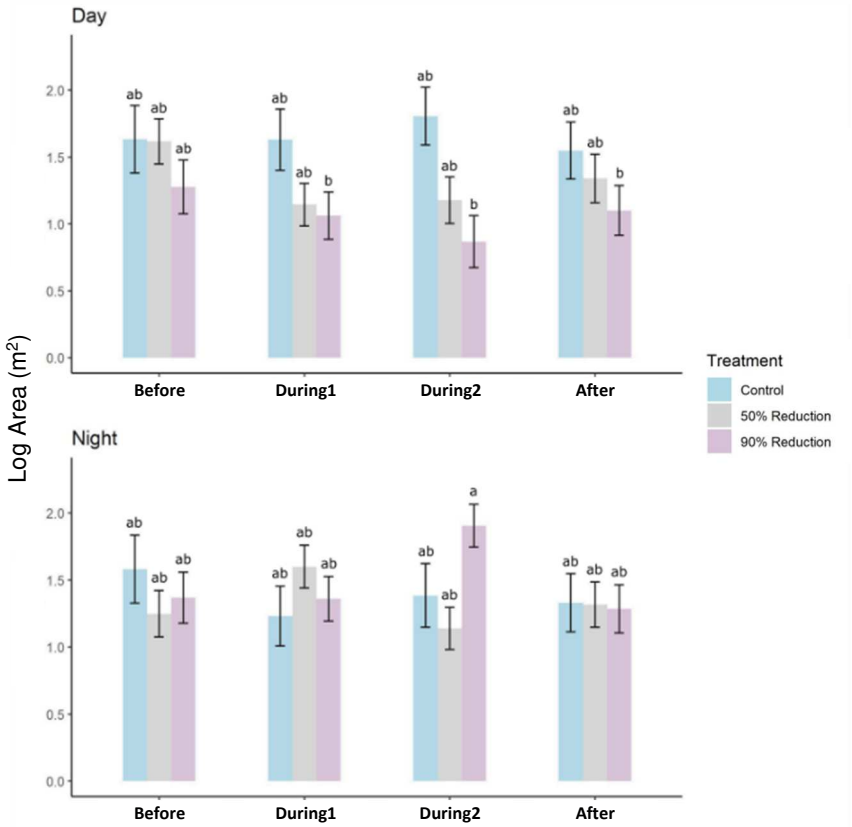

Figure 4.10: Influence of the experimental discharge reduction treatments on mean (± standard error) log area (m^2) used by 0+ trout in the day and at night. Results of Tukey's post hoc comparisons shown: mean values sharing the same letter are not significantly different.

4.3.3 1+ trout

The experimental discharge reduction resulted in significant differences in the absolute water depth and velocity used by 1+ trout over the detection periods (Table 4.1a). Within both During detection periods, 1+ trout within the 50% and 90% discharge reduction treatments were located in significantly shallower water compared with the Before detection period whereas there was no change in the Control treatment (Figure 4.11). In addition, 1+ trout within the 90% reduction treatment occupied significantly slower water compared with the Before detection period whereas there was no change in the Control or 50% reduction treatments (Figure 4.12). There was no difference in absolute water depth and velocity used by 1+ trout between the Before and After detection periods across all treatments (Figure 4.11 & Figure 4.12).

There were no significant differences in the relative water depth or velocity used by 1+ trout within treatments over the detection periods (Table 4.1b). In addition, discharge reduction had no effect on site loyalty (Table 4.2).

Discharge reduction resulted in significant differences in the area used by 1+ trout (Table 4.4). Although the Tukey's post hoc test could not identify differences in the absolute values between treatments over detection periods ($p > 0.05$), the data suggest that After discharge reinstatement, 1+ trout that had experienced a 90% discharge reduction were occupying a larger area compared with the Control treatment (Figure 4.13).

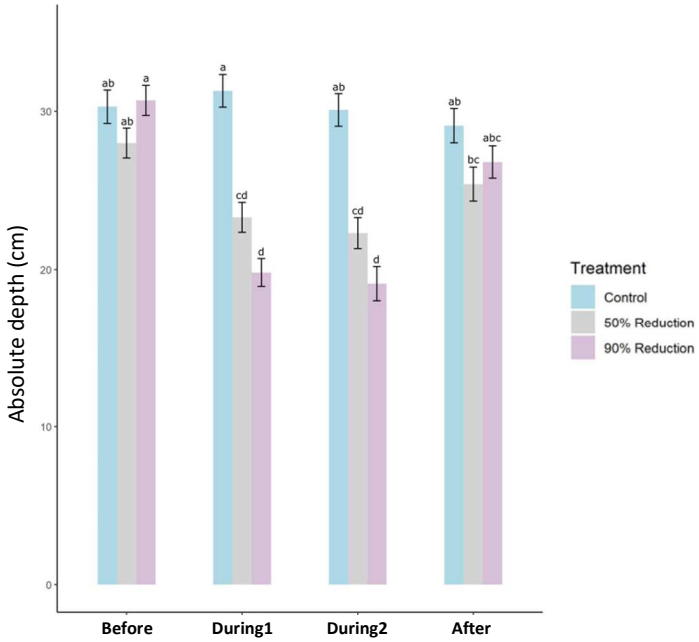

Figure 4.11: Influence of the experimental discharge reduction treatments on mean (± standard error) absolute depth (cm) used by 1+ trout. Results of Tukey's post hoc comparisons shown: mean values sharing the same letter are not significantly different.

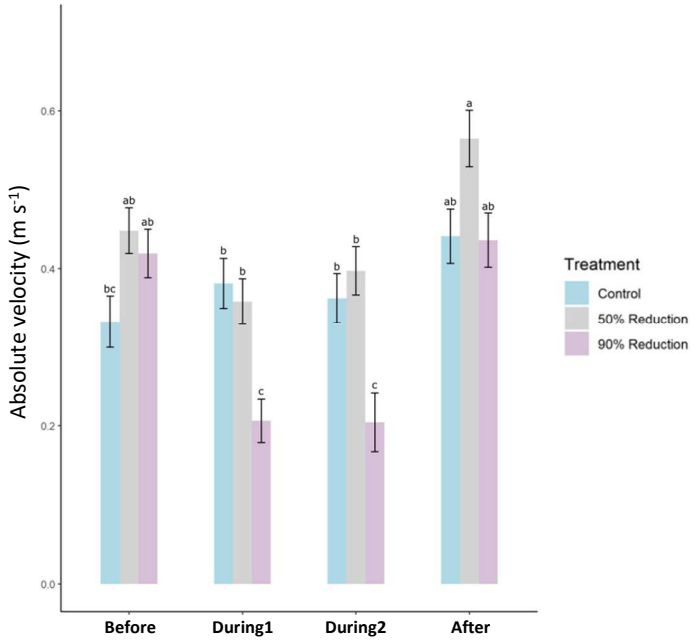

Figure 4.12: Influence of the experimental discharge reduction treatments on mean (± standard error) absolute velocity (m s^{-1}) used by 1+ trout. Results of Tukey's post hoc comparisons shown: mean values sharing the same letter are not significantly different.

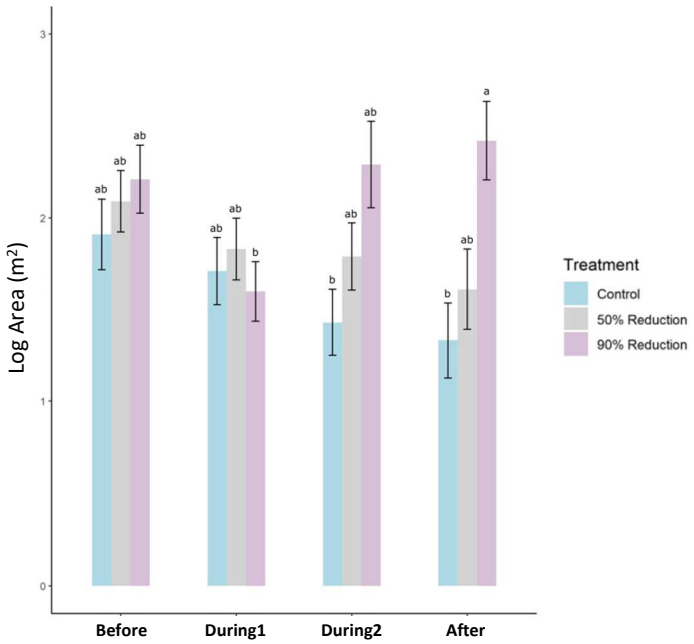

Figure 4.13: Influence of the experimental discharge reduction treatments on mean (± standard error) log area (m^2) used by 1+ trout. Results of Tukey's post hoc comparisons shown: mean values sharing the same letter are not significantly different.

4.3.4 ≥2+ trout

The experimental discharge reduction resulted in significant differences in the absolute water depth and velocity used by ≥2+ trout over the detection periods (Table 4.1a). Within both During detection periods, ≥2+ trout within the 90% reduction and 50% reduction treatments occupied shallower water compared with the Before detection period, whereas there was no change in the Control (Figure 4.14). In addition, ≥2+ trout in both During periods within the 90% reduction treatment were located in significantly slower water compared with the Before detection period, whereas there was no change in the Control and 50% reduction treatments (Figure 4.15). There was no difference in the absolute water depth and velocity used by ≥2+ trout between the Before and After detection periods across all treatments (Figure 4.14 & Figure 4.15).

There was a significant difference in the relative water velocity used by ≥2+ trout within treatments across detection periods (Table 4.1b). Although the Tukey's post hoc test could not identify differences ($p > 0.05$), the data suggest that in both During detection periods, ≥2+ trout within the 50% reduction treatment used relatively slower water and ≥2+ trout within the 90% reduction treatment used relatively faster

water compared with the Before detection period (Figure 4.16). Once discharge was reinstated, the data suggest that ≥2+ trout within the 50% reduction treatment used relatively slower water but fish within the Control and 90% reduction treatments used relatively faster water compared with what they used in the Before detection period (Figure 4.16).

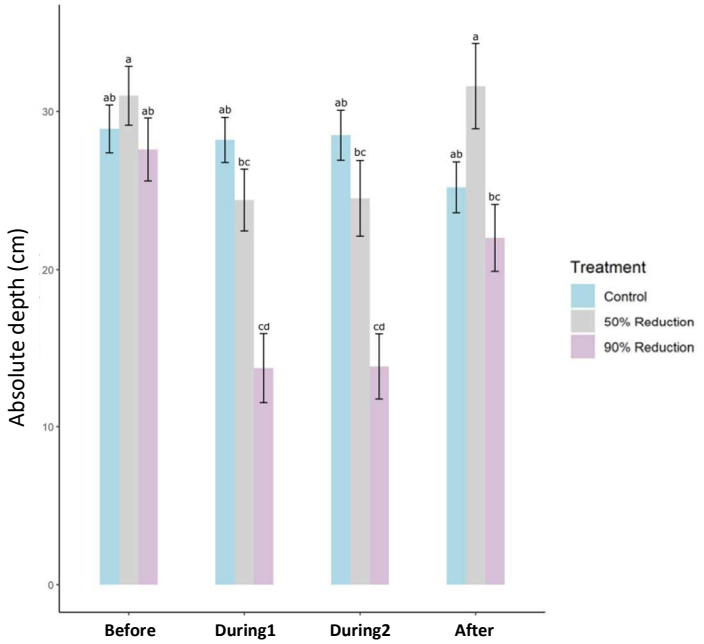

Figure 4.14: Influence of the experimental discharge reduction treatments on mean (± standard error) absolute depth (cm) used by ≥2+ trout. Results of Tukey's post hoc comparisons shown: mean values sharing the same letter are not significantly different.

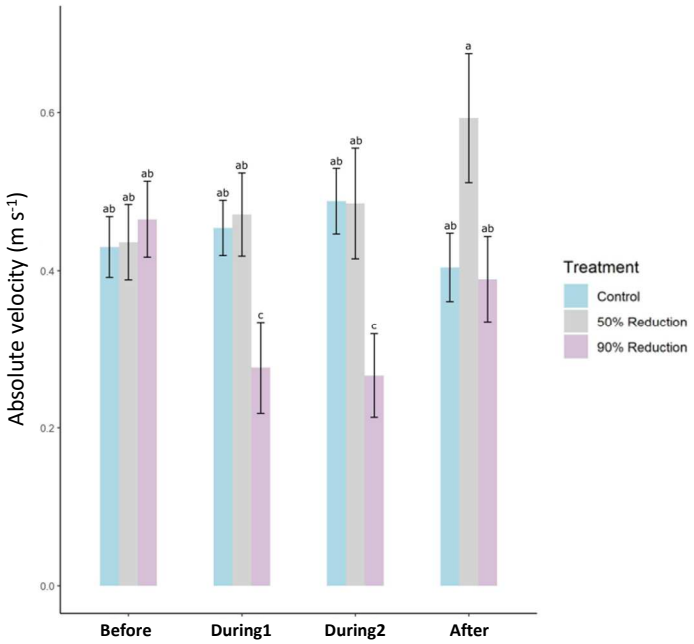

Figure 4.15: Influence of the experimental discharge reduction treatments on mean (± standard error) absolute velocity (m s^{-1}) used by ≥2+ trout. Results of Tukey's post hoc comparisons shown: mean values sharing the same letter are not significantly different.

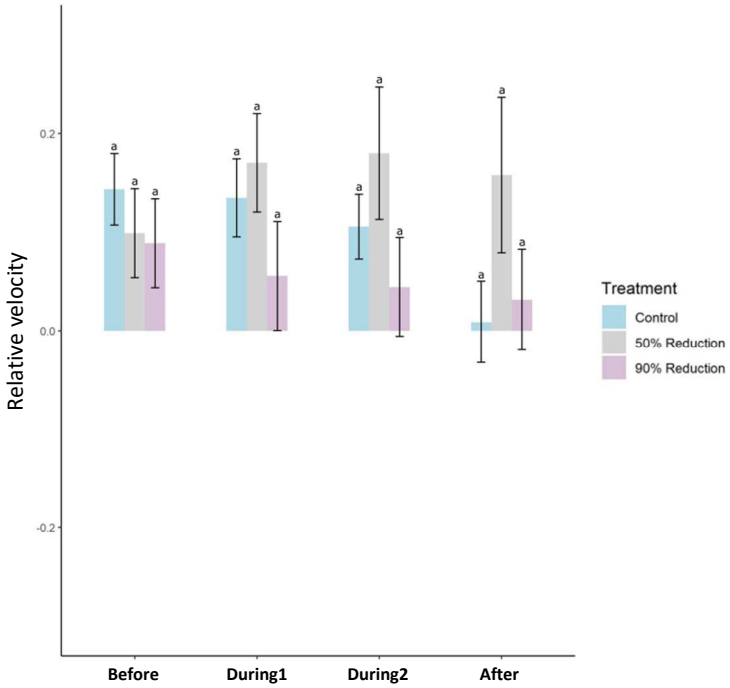

Figure 4.16: Influence of the experimental discharge reduction treatments on mean (± standard error) relative velocity used by ≥2+ trout. Results of Tukey's post hoc comparisons shown: mean values sharing the same letter are not significantly different.

The experimental reduction in discharge resulted in significant differences in the absolute and relative water velocity used by ≥2+ trout over the detection periods during the day compared with the night (Table 4.1a&b). Although the Tukey's post hoc test could not identify differences in the absolute values between treatments over detection periods in the day and at night ($p > 0.05$), the data suggest that there was a significant increase in the absolute velocity used by ≥2+ trout at night within the control treatment in the After detection period compared with the day (Figure 4.17). Within the control treatment Tukey's post hoc test identified that ≥2+ trout were located in relatively slower water in the After detection period in the day compared to the Before, this difference was not apparent at night (Figure 4.18).

There was a significant difference in site loyalty for ≥2+ trout between the Before and During1&2 detection periods among treatments (Table 4.2), where 81.9% of fish moved away from the mode antennae during a 90% discharge reduction compared with 42.1% in the Control (Table 4.3; Tukey's post hoc test $p < 0.01$). There were no lasting effects of discharge reduction on site loyalty for ≥2+ trout (Table 4.2b). In addition, there were no detectable effects of experimental discharge reduction on the area used by ≥2+ trout over the detection periods (Table 4.4).

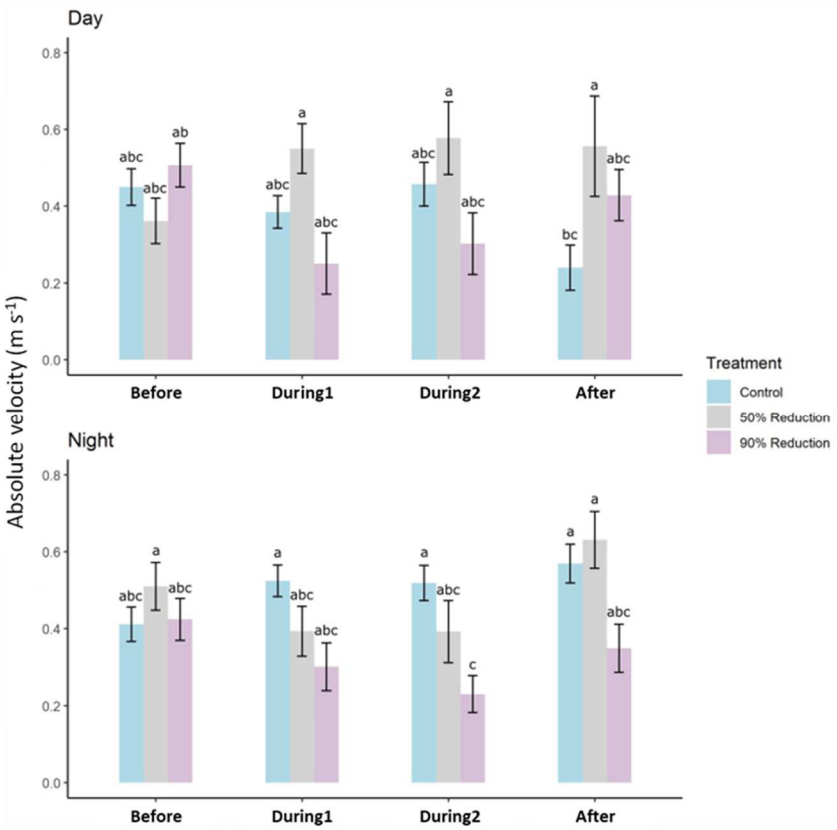

Figure 4.17: Influence of the experimental discharge reduction treatments on mean (± standard error) absolute velocity (m s^{-1}) used by ≥2+ trout in both daytime and night-time. Results of Tukey's post hoc comparisons shown: mean values sharing the same letter are not significantly different.

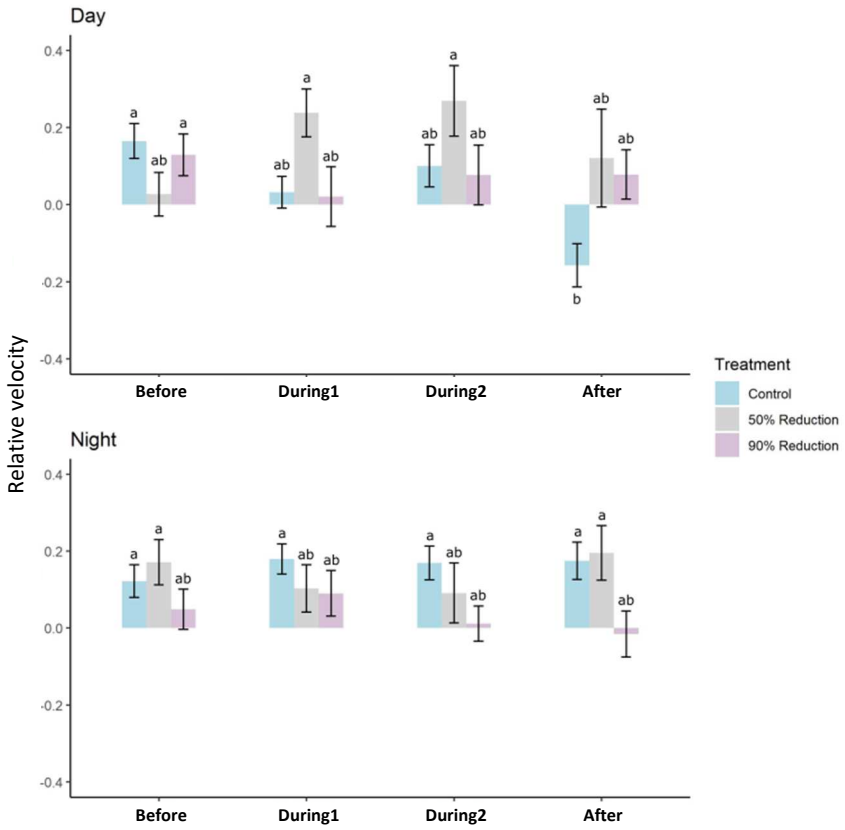

Figure 4.18: Influence of the experimental discharge reduction treatments on mean (± standard error) relative velocity used by ≥2+ trout during the daytime and night-time. Results of Tukey's post hoc comparisons shown: mean values sharing the same letter are not significantly different.

4.4 Discussion

The experimental 90% discharge reduction treatment, and to some extent the 50% reduction treatment, had a clear impact on the absolute water depths and velocities which salmonids occupied. Salmonids within the reduction treatments occupied shallower water with slower absolute velocities. This reflects the impact that the discharge reduction had on the instream habitat and, hence, the habitat available to the fish (Chapter 2).

Within the current investigation, during the 90% discharge reduction, salmon and 0+ trout occupied relatively shallower water compared with before. This finding is contrary to those of Armstrong *et al*. (1998), who reported that during severe droughts salmon par move to deeper habitats. Both salmon and 0+ trout site loyalty decreased between the Before and both During detection periods in the 90% reduction treatment. It is likely that, as a result of increased fish density under reduced discharge conditions, salmon and 0+ trout were pushed into shallow peripheral stream areas by more dominant older cohorts, due to increased competition for space and preferential

feeding habitats (Kahler *et al*., 2001). For both salmon and 0+ trout effects of discharge reduction on habitat use were transitory indicated by the lack of lasting (Before-After) effects.

Increased competition and fish density, during the 90% discharge reduction, may have decreased the stream area utilised by 0+ trout during the day to reduce predation risk by older salmonids: piscivory by older fish increased under reduced discharge conditions (Chapter 3). Young of the year (0+) trout may have also reduced the area used in the day as they were potentially more susceptible to attacks by avian predators under such conditions (Hostetter *et al*., 2012). It appears that 0+ trout increased the area used at night, where foraging is safer but less efficient (Reebs, 2002; Railsback *et al*., 2005), to compensate. Even though diel patterns and salmonid behaviour have been well documented (Fraser *et al*., 1995; Metcalfe *et al*., 1999; Bardonnet & Baglinière, 2000; López-Olmeda *et al*., 2012), results from this investigation do not support diel variation activity in salmonids as strongly as others (see Riley *et al*., 2006; Riley *et al*., 2009a).

In this investigation, area used by 1+ trout increased after the 90% reduction treatment had been reinstated, compared with the control. Stream area used is often inversely related to food abundance (Slaney & Northcote, 1974; Keeley, 2000), however, the flow reduction treatments did not cause a significant change in the density of prey (Chapter 2 & 3). Reinstatement of discharge would have created new habitats, due to the increase in wetted width (Chapter 2), giving fish the opportunity to expand their stream area used, which may have included new foraging sites (Grant *et al*., 2017), where larger prey items were consumed (Chapter 3). In addition, 1+ trout had high site loyalty under reduced discharge conditions, indicating that they adopt a 'sit it out' strategy remaining in the area/habitats that they know (Riley *et al*., 2009a; Gunnarsson & Steingrímsson, 2011; Nislow & Armstrong, 2012), suggesting resistance to reduced discharge conditions.

Unlike salmon and 0+ trout, where discharge reduction resulted in individuals occupying relatively shallower water, discharge reduction treatments resulted in a contrasting response in the relative velocity occupied by ≥2+ trout. The data suggest that during the 50% discharge reduction ≥2+ trout occupied relatively slower water but

during the 90% discharge reduction they occupied relatively faster velocities, compared with the habitats they had occupied before the discharge reductions. In addition, site loyalty decreased within the 90% reduction treatment, as a result of individuals seeking habitats with faster relative velocities. This may have increased movement out of the stream as they search for more suitable habitats (Chapter 5). Riley *et al*. (2009a) imposed a discharge reduction treatment to c.7% of the normal mean discharge on a small English chalk stream (Brandy Stream), where they reported that 2+ trout sought faster relative water velocities under reduced discharge compared with the patches they had occupied prior to discharge manipulation. Gowan & Fausch (2002) reported that changes in discharge altered the location of optimal feeding sites, which could go some way to explain why, in this study, under the discharge reduction treatments, different relative velocities were occupied. Within the 50% reduction treatment ≥2+ trout may have moved into relatively slower water due to increased benthic foraging (Kalleberg, 1958; Railsback *et al*., 2005). Following discharge reinstatement after the 50% discharge reduction ≥2+ trout remained in relatively slower water velocities. As inferior fish are often pushed out into marginal habitats with lower water velocities, it is likely that they were easy prey for ≥2+ trout and led to increased piscivory (Chapter 3). As discharge reduction had no impact on stream area used by ≥2+ trout this suggests that these optimal feeding sites were either already encompassed within their area, as older trout have a high range of movement (Riley *et al*., 2006), or they moved to new areas, encompassing these optimal feeding sites, and left areas that were no longer beneficial (Slavik *et al*., 2018). These findings are in contrast with Riley *et al*. (2009a) who reported that discharge reduction decreased the range of movement (stream area used) by ≥2+ trout. In general, there were few marked lasting effects of discharge reduction on ≥2+ trout habitat use, indicating that they are resilient to such conditions.

Chalk streams have high microhabitat overlap compared with other river systems (Watkins *et al*., 1997). This enables versatile habitat use by chalk stream salmonids under reduced discharge and for such fish to display a high degree of plasticity where there was not one overall direction in the response. Yearling (1+) trout deployed a ‘sit it out’ strategy indicating resistance to reduced discharge conditions. In

contrast, salmon, 0+ trout and ≥2+ trout reduced site loyalty under a 90% discharge reduction. No lasting effects of reduced discharge on site loyalty for all species/cohorts, despite all treatments undergoing salmonid capture and gut flushing protocol, and limited lasting effects of other habitat use variables, indicate that salmonids within this investigation were able to adapt to short term drought conditions.

4.5 Conclusion

Reduced discharge resulted in changes in habitat conditions such that salmonids were located in reduced absolute water depths and velocities (hypothesis 1), although there was evidence that salmonids (excluding 1+ trout) occupied habitats that had different relative depths and velocities compared with those they had occupied before the discharge was reduced (hypothesis 2). Salmon, 0+ and ≥2+ trout site loyalty reduced as they either moved into relatively shallower (salmon and 0+ trout) or relatively faster (≥2+ trout) habitats under a 90% discharge reduction (hypothesis 3). Discharge reduction had limited effect on salmonid stream area used (hypothesis 4). Diel day/night differences in habitat use, site loyalty and stream area used did not increase substantially for salmon, 1+ and ≥2+ trout, however stream area used by 0+ trout decreased in the day under a 90% discharge reduction (hypothesis 5). Despite the changes in habitat use during the discharge reduction there were almost no lasting effects of reduced discharge on habitat use indicating that salmonids are resilient, with 1+ trout resistant, to such conditions (hypothesis 6).

This study provides insight into habitat use by salmonids in chalk streams and how it is affected by reduced discharge conditions. In view of the predicted changes in precipitation, abstraction and river discharge, the results suggest that substantial undesirable impacts are not apparent, despite the scale of the imposed discharge reductions. Chalk stream salmonids appear to be highly resilient to the changed conditions, however, discharge reduction studies of a longer duration should be conducted to inform management on issues such as flow prioritisation, if needed. This is especially important for juvenile salmonids within smaller chalk streams as these are considered to be ideal nursery habitats, and small streams are more vulnerable to anthropogenic pressures and the impacts of climate change (Riley *et al.* 2018).

Chapter 5: Individual to Population: Effects of summer discharge reduction in chalk streams on wild salmonid size, growth rate, movement and population size.

5.1 Introduction

Unlike most mammals and birds, fish have the potential to grow throughout their lifespan (Reznick *et al*., 2002). Within fisheries science, growth is the gradual increase in mass over time (Ricker, 1979; Hopkins, 1992). Growth is key for the development of salmonids and is influenced by both abiotic (such as water temperature, velocity and depth) and biotic (such as food availability, competition and behaviour) factors (Fausch, 1984; Bear *et al*., 2007; Xu *et al*., 2010; Fernandes *et al*., 2015). Habitats with low water velocities which reduce prey delivery (Höjesjö *et al*., 2015), can impact growth rates. Therefore, growth rate can be maximised by occupying stream habitat that allows for maximum prey intake whilst minimising energy expenditure (Fausch, 1984). Greater growth is usually achieved by increased foraging effort, but this requires more energy expenditure and potentially leads to greater predation risk (Biro *et al*., 2006). Selecting habitats with sufficient cover and refuge will limit predation risk and increase the likelihood of salmonids transitioning to their next life stage.

As quantifying growth requires repeat measurements of individuals, mean length, mass and condition of populations are often used to determine how preceding environmental conditions have affected the population (Cowx & Fraser, 2003), where at a given length, heavier fish are considered to be in better condition than their lighter weight counterparts (Sutton *et al*., 2000). Mann *et al*. (1989) reported that salmonids of chalk streams grow at a faster rate and have higher levels of condition, than those of freshet streams, as chalk streams have attributes that promote the growth of salmonids (e.g. stable flows and temperatures, and productive food supplies; see Chapters 2 & 3).

In recent decades, populations of salmonids, including those in chalk streams, have come under threat as a result of increased pressures from anthropogenic activity (Acreman *et al*., 2008; Johnson *et al*., 2009). Human population growth has increased

the demand for water – particularly in the summer, which has resulted in frequent occurrences of low river discharge, which are further exacerbated by climatic change (Jonsson & Jonsson, 2009; Bowles & Henderson, 2012; Warren *et al*., 2015; Carlson *et al*., 2017; Rosenfeld, 2017). In addition, increased farming intensity has reduced water quality and quantity (Reaney *et al*., 2011; Lange *et al*., 2014). Anthropogenic influences impact natural river discharge regimes, thus altering the physical conditions and potentially having a negative impact on salmonid populations (Macnaughton *et al*., 2015).

Habitat loss is a fundamental impact of discharge reduction (White *et al*., 2016). Lower water depths and narrower wetted widths reduce lateral and longitudinal connectivity, thus limiting habitat availability under reduced discharge conditions (Boulton, 2003; Lake, 2003). Reduced habitat availability can concentrate fish and increase competition (Power *et al*., 2013) as well as predation risk from avian predators (Kennedy & Greer, 1988) and older fish (see Chapter 3; Keeley & Grant 2001; Hyvärinen & Huusko, 2006).

Salmonid growth has been reported to be lower during reduced discharge conditions (VerWey e*t al*., 2018), where low growth of salmonids could be attributed to low summer in-stream productivity and reduced prey for fish (Boulton, 2003; Wood & Armitage, 2004). Gries & Juanes (1998) reported that salmonids stop eating entirely under reduced discharge conditions, which would negatively impact fish growth rate. However, this study did not verify their findings: the results presented in Chapter 3 indicated that feeding is maintained during reduced discharge conditions through plasticity of diet choice. Stream-scale experiments are needed in order to determine how reduced discharge affects salmonid growth rate if prey availability is not limited and if feeding is maintained.

Decreases in available habitat, due to reduced discharge, may increase injuries and mortalities associated with between cohort aggression (Lindeman *et al*., 2015), as salmonid behaviour is influenced by territoriality/dominance hierarchies (Fausch, 1984; Sloman & Armstrong, 2002). As well as mortality via predation and cohort aggression, loss of individuals from a population can occur via movement in and out of the affected area. Salmonids might move out of their home stream reach under

reduced discharge conditions due to a reduction in a) territory size, b) increased competition, both as a result of elevated population density, and c) reduced habitat quality directly caused by reduced discharge. Under experimental laboratory conditions, fish frequently show strong movement responses to reduced discharge (Kraft, 1972; Davey *et al*., 2006), but results of movement under more natural field conditions vary (Kahler *et al*., 2001). Riley *et al*. (2009a) reported that, within a UK chalk stream (Brandy stream), reduced discharge resulted in no net downstream movement of 0+ salmonids, as they adopted a 'sit it out' tactic, possibly because the optimal response is for fish to stay in their established territory if still available (Davey & Kelly, 2007; Fornaroli *et al*., 2016), so population redistribution may not be necessary (Kemp *et al.,* 2003), whereas VerWey *et al*. (2018) report that during drought, trout move upstream in search of deeper habitats. Replicated stream-scale experiments are needed to determine how reduced discharge conditions affect salmonid movement and if this movement influences the loss rate of individuals from the population.

Overall the size of a salmonid population is determined by the balance between reproduction, mortality, and migration (in and out of the stream). The carrying capacity of streams will be dictated by their physical attributes (Armstrong *et al*., 2003; Gallagher *et al*., 2014). Although reduced discharge conditions can result in increased densities of salmonids (Kahler *et al*., 2001), the extent to which population density is affected can vary from year to year (Elliot *et al*., 1997). Life cycle models predict that more frequent extreme low discharge events, especially low summer discharge, will significantly reduce the density of salmonids over time (see Ohlberger *et al*., 2018). In order to verify model predictions, stream-scale studies are needed to determine if reduced discharge has consistent lasting effects on salmonid population density.

Salmonid populations, including those in chalk streams, are of great ecological and economic importance to the UK (Cowx *et al*., 2009), but are increasingly threatened by the current and projected rise in pressures from anthropogenic activity (Winfield, 2016). Consequently, understanding the relationship between reduced discharge and salmonid growth, along with movement, loss rate and population size and density, represents a major goal for fisheries management.

This chapter explores the effects of experimental discharge reduction on wild salmon and trout. Five hypotheses were tested: 1) decreases in water depth, velocity and wetted width, as a result of discharge reduction, will reduce salmonid growth, 2) reduced discharge will result in elevated levels of movement out of the affected stream area, 3) reduced discharge conditions will increase the loss rate of individuals from the population, 4) reduced discharge will have lasting negative effects on salmonid population size and density, and 5) salmonid growth response to discharge reduction will reduce among streams that is related to the extent of physical change (which in turn is influenced by the stream profile – abiotic variables).

5.2 Methods

The investigation took place over three years. In each year, two of the three streams were subject to an experimental discharge reduction (50% or 90%). For information on the study site and a detailed explanation of the discharge manipulation, see section 1.5.

5.2.1 Salmonid capture and tagging

Salmonids were captured using electrofishing (for a detailed description see section 3.2.1), within defined sections in each of the three study streams (see Figure 5.1). Sections were electrofished consecutively in an upstream direction and at the end of the final section was a sluice gate (see Sluice gate on Figure 5.1). Although stop-nets could have been used to prevent fish moving between sections, when electrofishing was undertaken, sections were not analysed separately and the waters force entering each stream under the sluice gate prevented any fish escaping out of the study streams into the canal. In addition, it has been reported that where the width of the stream is small in relation to the length of stretch fished, the usefulness of stop-nets is low (Bohlin *et al*., 1989; Niemela *et al*., 2000). Thus, using stop-nets for this study would have been labour intensive and would have had limited bearing on subsequent analytical results.

All untagged individuals captured during the Before occasion had a PIT tag implanted (see section 4.2.1 for detailed methods of PIT tagging) prior to their fork length (to nearest 1 mm) and weight (to nearest 0.1 g) being recorded. Within the

During and After occasions all individuals captured were scanned for the presence of a PIT tag and, if present, the PIT tag code was recorded. Length and weight measurements were also taken from all individuals. The unique PIT tag code enabled growth rate calculation as the length and weight of individuals could be tracked.

5.2.2 Temperature

Temperature data used was recorded by the Tinytag logger deployed at the top of each stream reach, as described in Chapter 2 (see section 2.2.1; Figure 5.1).

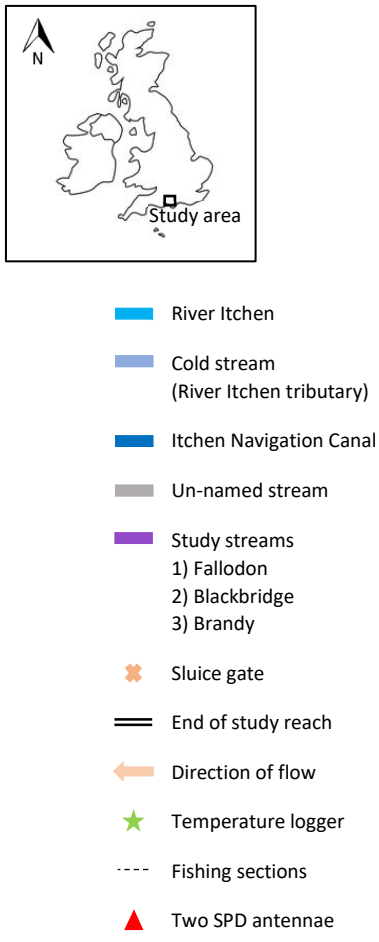

Figure 5.1: Map displaying the location of the different sites, extent of study streams, location of the temperature loggers, SPD antennae and electrofishing sections on Brandy stream. OS maps accessed 27/02/2019.

5.2.3 Data preparation

Over the three experimental years a total of 7,219 salmonid were caught. To keep alignment with previous chapters, salmon aged 0+ and 1+ were combined for the analysis and trout aged 2+ and older were merged into a ≥2+ trout cohort (see Table A4.1 for total number of fish caught in each treatment, stream and occasion).

Salmonid growth rate and condition

Growth rate was determined from the change in mass of PIT tagged individuals over time. PIT tagged individuals that were caught in both the Before and During occasions were used to investigate the effect of discharge reduction on growth rate and individuals caught within the Before and After occasions were used to investigate any lasting effects of the discharge reduction once discharge had been reinstated. Growth rates of tagged individuals that were caught on all three occasions were investigated to see if there were any specific effects of discharge reduction on these individuals over the whole experimental period and to verify the two responses to discharge reduction tested (Before-During growth and Before-After growth). If growth rate between Before-During differs from Before-After it may be because a) the During-After period had a real influence on the average growth rate over Before-After, or b) they were different fish. Analysing growth of tagged individuals caught on all three occasions allowed for the influence of During-After to be compared and removes the possibility of b) having an effect. Within the same year, any individuals that were tagged in one stream but subsequently recaptured in another stream were removed from the analysis (total of 9 individuals), as these individuals could not be clearly attributed to any one treatment.

When analysing growth rate, the influence of the initial size of individuals and any differences in temperature between streams and years were taken into account by calculating the relative growth rate (RGR) of individuals (Hoffmann & Poorter, 2002; Wolnicki *et al*., 2006):

$$\%\, RGR \;=\; \left(\frac{(ln\, M_2 \;-\; ln\, M_1)}{Degree\ Days}\right) x\, 100 \qquad (1)$$

Where M_2 is mass (g) at time 2, M_1 is the mass (g) at time 1, and Degree days is the sum of the daily mean stream temperature between electrofishing occasions.

For all captured salmonids (tagged and untagged), condition was calculated using Fulton's condition index K (Froese, 2006):

$$\mathrm{K} = (\mathrm{Mass\ (g)\ x\ 100})/\mathrm{Length\ (cm)}^3 \quad (2)$$

Movement

Two Single Point Decoder (SPD) PIT antennae are installed in series at each of the three exits of the Brandy Stream (see SPD antennae on Figure 5.1). These antennae detected the movement of PIT tagged salmonids 'in' and 'out' of this study reach. Salmonid movements were determined by applying consistent criteria as to what constituted a 'movement'. Fish with repeated detections over one pair of antennae were excluded, as these were thought to have established home ranges near the antennae. Where possible, fish location was confirmed following subsequent electrofishing surveys.

Estimated population size and density (including tagged and untagged individuals)

Estimated 'population' size (EPS) of each species/cohort within each defined electrofishing section in the Before and After sampling occasions were calculated for each stream and treatment. Population sizes were estimated using depletion catch and the Zippin method (Zippin, 1956) within the Fisheries Stock Assessment package in R (Ogle *et al*., 2018). Whole stream EPS was obtained by summing the estimates from the defined electrofishing sections within each stream. The standard errors of EPS in each section were squared, and the square root of the sum was taken to give the standard error of stream EPS (Hogan, 2006; Ueding, 2012). Relative change in EPS between the Before and After occasions in each stream was then calculated for each cohort:

$$Relative\ change\ in\ EPS = \frac{(After\ -\ Before)}{Before} \quad (3)$$

'Population' density was calculated by dividing the population estimate for the Before and After occasions by the stream area (stream length x mean wetted width;

see section 1.5.1 for values) and multiplying it by 100 to give density per 100 m^{-2} for each species/cohort. Relative change in 'population' density was calculated using equation (3). It was not possible to calculate EPS and density for the During occasion which was performed purely to collect gut contents samples.

5.2.4 Statistical analysis

Growth rate of tagged individuals

Analysis of variance based on linear models was used to examine the effect of experimental discharge reduction on the growth rate of PIT tagged individuals for each species/cohort, to determine if the discharge reduction treatments had any effect (Before-During) or lasting impact (Before-After) on growth rates (see Table 2.2 – for explanation of statistical models used to determine the effects of discharge reduction and lasting effects of discharge reduction once discharge had been reinstated). Tukey's post hoc test was then used to identify where the significant differences between the means lay.

As the mass of an individual needs to be measured on two separate occasions to calculate a growth rate, the analysis only included the factors Year and Treatment. The analysis was then repeated to include the individual streams as a factor, where the interaction (i.e. Treatment:Stream) would determine if there was any significant difference in the response of growth rate to the discharge reduction treatments among the different streams (see Table 2.1 & 2.2 – for breakdown and explanation of experimental factors and interactions).

The growth rate of PIT tagged individuals that were caught on all three occasions within one experimental year (total of 514 fish; see Table A4.2) were investigated to see if there were any effects of Treatment:Occasion and Treatment:Occasion:Stream on these individuals over the whole experimental period. Growth rate between Before-During and During-After occasions were compared.

Mean length, mass and condition

For each experimental factor (Year, Treatment*Occasion) the influence of the experimentally reduced discharge and any lasting effects on the size and condition of

salmonids (tagged and untagged individuals) were investigated. Analysis of variance based on linear models with Tukey's post hoc test was used to examine the effect of the experimental discharge reduction on mean length, mass and condition for each species/cohort. Length is a potential surrogate for structural mass, mass comprises both structural and reserve tissues and condition gives an indication of fish health and assumes that at a given length fish of heavier mass are in better condition. Data were log transformed where necessary. The analysis was then repeated to include the individual streams as a factor, where the interaction (i.e. Treatment:Occasion:Stream) would determine if there was any significant difference in the response of mean length, mass and condition to the discharge reduction treatments among streams.

Loss rate

Weekly loss rates were determined for each species/cohort against initial (Before) density to ascertain if there were any effect of reduced discharge on population size and density.

Movement

In Brandy stream 'In' and 'out' movements were calculated as a percentage of the Before population estimates when all fish caught were tagged. Any PIT tags detected moving upstream on the pair of SPDs were considered 'in' movements and any PIT tags detected moving in a downstream direction were considered 'out' movements.

Estimated population size and salmonid density

The relative change in EPS and salmonid density for salmon and each trout cohort as a result of the different discharge treatments was analysed using ANOVA based on linear models with Tukey's post hoc tests. The relative changes in EPS and salmonid density for the individual streams were treated as replicates, Treatment and Cohort were factors within the model.

All analysis was carried out in R-studio version 3.0.3 (R Core Team, 2018).

5.3 Results

5.3.1 Salmon

The experimental discharge reduction did not have any significant effect on the growth rate of salmon (Table 5.1). Furthermore, no significant effects were detected when stream was included in the model (Table 5.2).

There were no detectable effects of experimental discharge reduction on mean length and mass of salmon within treatments across occasions (Table 5.3 & Table 5.4). A significant effect of the experimental discharge reduction was detected on the mean condition of salmon (Table. 5.3). Tukey's post hoc tests identified that the differences were within the During occasion between treatments and not within treatment over time, (Figure A4.1).

There was a significant lasting effect of reduced discharge on the mean condition of salmon (Table 5.4), where the mean condition of salmon following the Control treatment was lower but there was no change after either of the discharge reduction treatments (Figure 5.2).

Within Brandy Stream, during the 90% discharge reduction 37.5% of salmon moved out of the experimental area compared with 3.1% during the control treatment. After the 90% discharge reduction, there was a movement of 13.2% of salmon into the study area compared with no movement in the control treatment (Table 5.5).

Table 5.1: Results of ANOVA testing the effects of reduced discharge and lasting effect of reduced discharge on relative growth rates of salmonids.

	Growth rate									
	Before - During					Before - After				
Source	**df**	**ss**	**ms**	**F**	***p***	**df**	**ss**	**ms**	**F**	***P***
Salmon										
Year	2	.015	.0075	11.85	***	2	.025	.0125	18.45	***
Treatment	2	.001	.0009	1.53		2	.002	.0014	2.15	
Residuals	45	.028	.0006			98	.066	.0001		
0+ trout										
Year	2	.003	.0016	2.46		2	.001	.0008	1.83	
Treatment	2	.001	.0007	1.16		2	.002	.0012	2.82	
Residuals	181	.119	.0006			261	.124	.0004		
1+ trout										
Year	2	.0005	.0002	1.61		2	.001	.0006	4.60	*
Treatment	2	.0021	.0010	5.88	**	2	.001	.0005	4.32	*
Residuals	296	.0524	.0001			556	.077	.0001		
≥2+ trout										
Year	2	.001	.0008	.58		2	.004	.002	1.74	
Treatment	2	.002	.0011	.79		2	.001	.001	.64	
Residuals	106	.152	.0014			184	.213	.001		

****p <0.001, **p <0.01, *p <0.05*, Blanks = *p >0.05*.

Table 5.2: Results of ANOVA testing stream effects of reduced discharge and lasting effect of reduced discharge on relative growth rate of salmonids.

	Growth rate									
	Before - During					Before - After				
Source	**df**	**ss**	**ms**	**F**	***p***	**df**	**ss**	**ms**	**F**	***P***
Salmon										
Year	2	.015	.0075	14.01	***	2	.025	.0125	18.11	***
Treatment	2	.001	.0009	1.81		2	.002	.0014	2.11	
Stream	2	.003	.0016	3.07		2	.001	.0008	1.21	
Treatment:Stream	2	.003	.0016	3.01		3	.001	.0001	.25	
Residuals	41	.022	.0005			93	.064	.0006		
0+ trout										
Year	2	.003	.0016	2.49		2	.0017	.0008	1.85	
Treatment	2	.001	.0007	1.17		2	.0026	.0013	2.85	
Stream	2	.001	.0007	1.11		2	.0018	.0009	1.92	
Treatment:Stream	8	.003	.0011	1.70		8	.0004	.0011	2.38	
Residuals	176	.115	.0006			251	.0224	.0004		
1+ trout										
Year	2	.0005	.0002	1.62		2	.0012	.0006	4.85	**
Treatment	2	.0021	.0010	5.96	**	2	.0012	.0005	4.54	*
Stream	2	.0001	.0003	.18		2	.0020	.0010	7.62	***
Treatment:Stream	8	.0041	.0003	1.83		8	.0021	.0010	7.89	***
Residuals	291	.0508	.0001			552	.0729	.0001		
≥2+ trout										
Year	2	.0016	.0008	.56		2	.0041	.0020	1.71	
Treatment	2	.0022	.0011	.76		2	.0015	.0007	.63	
Stream	2	.0011	.0005	.39		2	.0009	.0004	.41	
Treatment:Stream	8	.0001	.0001	.02		2	.0001	.0001	.02	
Residuals	102	.1510	.0014			180	.2127	.0011		

****p <0.001, **p <0.01, *p <0.05*, Blanks = *p >0.05*.

5.3.2 0+ trout

Similar to salmon, the experimental discharge reduction did not have a significant effect on the growth rate of 0+ trout (Table 5.1). Furthermore, no significant effects were detected when stream was included in the model (Table 5.2).

There were no detectable effects of experimental discharge reduction on mean length and mass of 0+ trout within treatments across occasions (Table 5.3). There was a significant effect of reduced discharge on the mean condition of 0+ trout (Table 5.3). Tukey's post hoc tests identified that there was a significant decrease in mean condition across all treatments (Figure A4.2). There were no apparent lasting effects of discharge reduction on 0+ trout mean length, mass and condition (Table 5.4).

Table 5.3: Results of ANOVA testing the effects of reduced discharge on mean length (cm), mass (g) and condition (K) of salmonids.

	Length (cm)					Mass (g)					Condition (K)				
Source	**df**	**ss**	**ms**	**F**	***p***	**df**	**ss**	**ms**	**F**	***P***	**df**	**ss**	**ms**	**F**	***p***
Salmon															
Year	2	15.36	7.68	134.81	***	2	140.59	70.29	127.50	***	2	.31	.15	26.74	***
Treatment	2	1.08	.54	9.55	***	2	10.80	5.40	9.79	***	2	.02	.01	2.14	
Occasion	1	.85	.85	15.03	***	1	7.23	7.23	13.11	***	1	.01	.01	1.31	
Treatment:Occasion	2	.06	.03	0.61		2	.91	.45	0.82		2	.04	.02	3.79	*
Residuals	460	26.21	.05			460	253.63	.55			460	2.69	.01		
0+ trout															
Year	2	.25	.12	4.83	**	2	1.27	.64	2.68		2	.41	.20	35.47	***
Treatment	2	.75	.37	14.56	***	2	5.71	2.86	12.05	***	2	.09	.05	8.00	***
Occasion	1	8.30	8.30	322.85	***	1	64.11	64.11	270.53	***	1	.39	.39	66.93	***
Treatment:Occasion	2	.09	.04	1.68		2	.50	.25	1.06		2	.04	.02	3.31	*
Residuals	2056	52.85	.03			2056	487.20	.24			2056	12.12	.01		
1+ trout															
Year	2	2.63	1.32	90.36	***	2	22.40	11.20	81.83	***	2	.29	.14	3.51	*
Treatment	2	.13	.06	4.45	*	2	2.03	1.01	7.41	***	2	.28	.14	3.42	*
Occasion	1	.45	.45	31.11	***	1	1.51	1.51	11.04	***	1	.41	.41	10.06	**
Treatment:Occasion	2	.01	.01	.33		2	.08	.34	.28		2	.03	.02	.39	
Residuals	1438	20.86	.01			1438	196.8	.14			1438	58.9	.04		
≥2+ trout															
Year	2	1.67	.83	27.64	***	2	18.48	9.24	29.25	***	2	.75	.38	4.21	*
Treatment	2	2.05	1.02	33.94	***	2	18.85	9.42	29.84	***	2	.22	.10	1.2	
Occasion	1	.01	.01	.17		1	.01	.01	.02		1	.09	.09	1.05	
Treatment:Occasion	2	.01	.01	.23		2	.51	.26	.81		2	.34	.17	1.91	
Residuals	497	14.98	.03			497	156.99	.32			497	44.46	.09		

****p <0.001, **p <0.01, *p <0.05*, Blanks = *p >0.05*.

Table 5.4: Results of ANOVA testing the lasting effects of reduced discharge on mean length (cm), mass (g) and condition (K) of salmonids.

	Length (cm)					Mass (g)					Condition (K)				
Source	**df**	**ss**	**ms**	**F**	***p***	**df**	**ss**	**ms**	**F**	***P***	**df**	**ss**	**ms**	**F**	***p***
Salmon															
Year	2	16.76	8.38	163.32	***	2	152.75	76.37	152.57	***	2	.35	.17	18.40	***
Treatment	2	.84	.42	8.25	***	2	8.18	4.09	8.17	***	2	.05	.02	2.57	
Occasion	1	2.06	2.06	40.29	***	1	15.434	15.43	30.82	***	1	.21	.21	22.06	***
Treatment:Occasion	2	.07	.03	.67		2	.32	.16	.31		2	.07	.03	4.10	*
Residuals	620	31.81	.05			620	310.37	.50			620	6.03	.01		
0+ trout															
Year	2	.60	.30	11.52	***	2	1.59	.79	3.33	*	2	1.65	.82	107.03	***
Treatment	2	.77	.39	14.94	***	2	5.83	2.92	12.22	***	2	.12	.06	7.66	***
Occasion	1	20.71	20.71	801.41	***	1	150.40	150.40	630.46	***	1	1.95	1.95	253.47	***
Treatment:Occasion	2	.12	.06	2.31		2	.93	.47	1.95		2	.01	.01	.33	
Residuals	2813	72.70	.03			2813	671.07	.24			2813	12.68	.01		
1+ trout															
Year	2	3.12	1.56	110.17	***	2	26.11	13.05	96.23	***	2	.46	.23	6.40	**
Treatment	2	.16	.08	5.72	**	2	1.90	.95	7.00	***	2	.11	.05	1.51	
Occasion	1	1.49	1.49	105.44	***	1	5.64	5.63	41.54	***	1	1.41	1.41	39.46	***
Treatment:Occasion	2	.05	.03	1.81		2	.70	.35	2.59		2	.12	.06	1.69	
Residuals	1880	26.63	.01			1880	255.03	.14			1880	67.35	.04		
≥2+ trout															
Year	2	2.01	1.01	31.39	***	2	21.05	10.53	33.81	***	2	.54	.28	3.61	*
Treatment	2	1.71	.85	26.66	***	2	15.15	7.57	24.32	***	2	.18	.09	1.24	
Occasion	1	.01	.01	.39		1	.01	.01	.01		1	.16	.16	2.12	
Treatment:Occasion	2	.18	.10	2.32		2	4.50	2.25	7.23	***	2	.42	.21	2.80	
Residuals	629	20.18	.03			629	195.85	.31			629	46.62	.07		

****p <0.001, **p <0.01, *p <0.05*, Blanks = *p >0.05*.

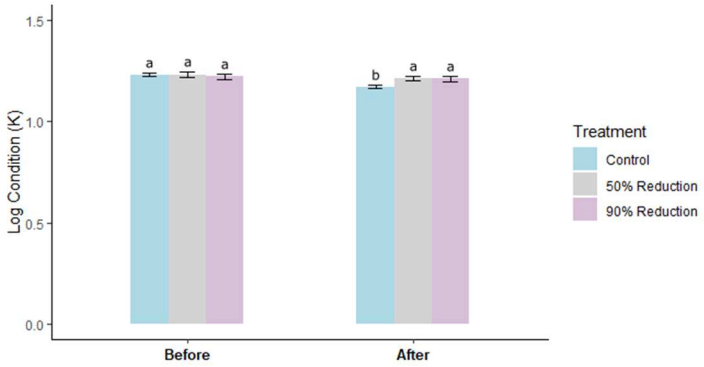

Figure 5.2: Lasting effects of experimental discharge reduction treatments on mean (±standard error) Log Condition(K) of salmon. Results of Tukey's post hoc comparisons shown: mean values sharing the same letter are not significantly different.

Table 5.5: Percentage (%) of the population that moved either in or out of Brandy stream within the different sampling occasions when different discharge treatments were imposed. nm = no movement.

	Salmon		0+ trout		1+ trout		≥2+ trout	
	In	Out	In	Out	In	Out	In	Out
Control								
Before	nm	5.4	nm	1.1	nm	nm	nm	2.9
During	nm	3.1	nm	4.3	nm	1.1	nm	1.6
After	nm	0.8	nm	0.6	nm	0.5	nm	1.0
50% reduction								
Before	nm	nm	nm	nm	nm	1.1	nm	2.1
During	nm	nm	nm	nm	nm	2.9	nm	3.7
After	nm	nm	nm	nm	nm	2.2	nm	2.0
90% reduction								
Before	nm	nm	nm	nm	nm	1.0	nm	nm
During	nm	37.5	nm	5.7	nm	8.8	nm	31.1
After	13.2	nm	nm	0.7	nm	0.9	nm	nm

There were significant differences among streams in the response of mean condition of 0+ trout to discharge reduction (Table 5.6). Mean condition of 0+ trout decreased in Brandy stream when it was a Control treatment and Blackbridge when it was a 50% reduction (Figure 5.3). Across all three streams mean condition of 0+ trout decreased when they were assigned a 90% reduction treatment. This indicates that treatment overrides any effects of stream as there were differences in mean condition amongst streams when assigned a control and 50% reduction treatment, but the response was the same in the 90% reduction treatment.

There was no substantial movement of 0+ trout in and out of Brandy stream as a result of discharge reduction (Table 5.5).

Table 5.6: Results of ANOVA testing stream effects of reduced discharge on mean length (cm), mass (g) and condition (K) of salmonids.

	Length (cm)					Mass (g)					Condition (K)				
Source	**df**	**ss**	**ms**	**F**	***p***	**df**	**ss**	**ms**	**F**	***P***	**df**	**ss**	**ms**	**F**	***p***
Salmon															
Year	2	15.36	7.68	141.81	***	2	140.59	70.29	133.81	***	2	.31	.15	27.27	***
Treatment	2	1.08	.54	10.04	***	2	10.80	5.40	10.27	***	2	.02	.01	2.18	
Occasion	1	0.85	.85	15.81	***	1	7.23	7.23	13.76	***	1	.01	.008	1.33	
Stream	2	.09	.04	.87		2	.93	.46	.88		2	.01	.007	1.19	
Treatment:Occasion:Stream	11	1.86	.16	3.12	***	11	17.72	1.61	3.06	***	11	.14	.01	2.31	**
Residuals	449	24.32	.05			449	235.88	.52			449	2.58	.01		
0+ trout															
Year	2	.25	.12	5.07	**	2	1.27	.63	2.82		2	.41	.21	35.99	***
Treatment	2	.75	.37	15.29	***	2	5.71	2.86	12.71	***	2	.09	.04	8.11	***
Occasion	1	8.29	8.29	338.99	***	1	64.11	64.10	285.58	***	1	.39	.39	67.92	***
Stream	2	1.73	.87	35.43	***	2	18.13	9.06	40.38	***	2	.12	.06	10.86	***
Treatment:Occasion:Stream	12	1.16	.09	3.95	***	12	10.74	.89	3.99	***	12	.16	.01	2.29	**
Residuals	2044	50.04	.02			2044	458.83	.22			2044	11.87	.005		
1+ trout															
Year	2	2.63	1.31	99.68	***	2	22.40	11.19	91.16	***	2	.29	.14	3.50	*
Treatment	2	.12	.06	4.91	**	2	2.02	1.01	8.25	***	2	.28	.14	3.41	*
Occasion	1	.45	.45	34.32	***	1	1.51	1.51	15.29	***	1	.41	.41	10.02	**
Stream	2	1.51	.75	57.30	***	2	16.58	8.29	67.49	***	2	.11	.06	1.35	
Treatment:Occasion:Stream	12	.61	.05	3.87		12	5.11	.42	3.47		12	.16	.01	.33	
Residuals	1426	18.83	.01			1426	175.18	.12			1426	58.66	.04		
≥2+ trout															
Year	2	1.67	.83	36.67	***	2	18.48	9.24	36.28	***	2	.75	.38	4.18	*
Treatment	2	2.04	1.02	45.03	***	2	18.85	9.42	37.02	***	2	.21	.10	1.19	
Occasion	1	.01	.01	.23		1	.008	.007	.03		1	.09	.09	1.04	
Stream	2	3.59	1.79	78.92	***	2	30.41	15.2	59.74	***	2	.16	.07	.86	
Treatment:Occasion:Stream	12	.37	.03	1.47		11	3.37	.30	1.20		11	.83	.07	.84	
Residuals	486	11.04	.03			486	123.71	.25			486	43.81	.09		

****p <0.001, **p <0.01, *p <0.05*, Blanks = *p >0.05*.

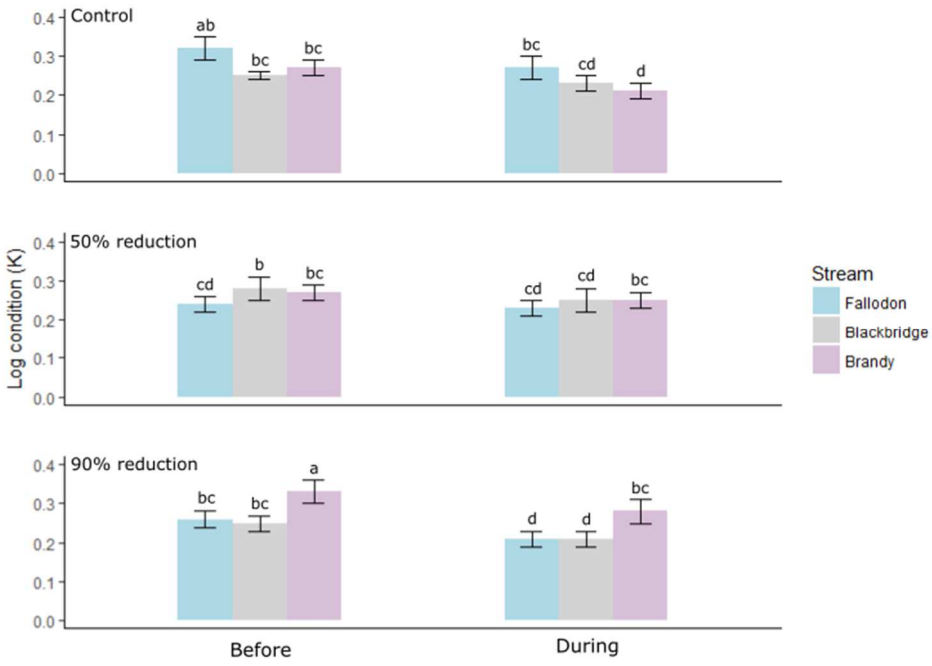

Figure 5.3: Influence of stream and experimental discharge reduction on mean (±standard error) Log Condition (K) of 0+ trout. Results of Tukey's post hoc comparisons shown: mean values sharing the same letter are not significantly different.

5.3.3 1+ trout

There were significant Before - During and lasting (Before-After) effects of reduced discharge on the growth rate of 1+ Trout (Table 5.1). Yearling (1+) trout had a significantly higher growth rate over the Before-During period when they were experiencing a 50% discharge reduction compared with the Control and 90% reduction treatments (Figure 5.4a). There was a corresponding significant lasting effect on growth rate in the 50% reduction compared to the Control (Figure 5.4b), which was also apparent within the 90% reduction treatment.

There were significant lasting differences among streams in the response of growth rate of 1+ trout to discharge reduction (Table 5.2; Figure 5.5). Growth rates of 1+ trout were significantly higher in Fallodon and lower in Brandy when they had experienced a 50% discharge reduction compared with the other two treatments.

Discharge reduction had no detectable effect on mean length, mass or condition of 1+ trout (Table 5.3 & Table 5.4). There was no substantial movement of 1+ trout in or out of Brandy stream as a result of discharge reduction (Table 5.5).

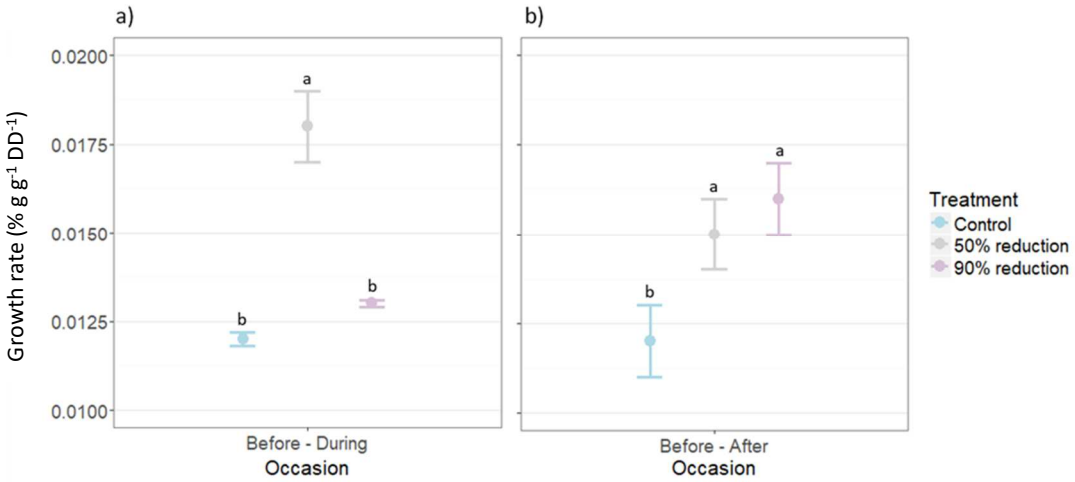

Figure 5.4: Influence of discharge reduction (a) and lasting effects (b) of experimental discharge reduction treatments on mean (±standard error) growth rate of 1+ trout (% g g^{-1} DD^{-1}). Results of Tukey's post hoc comparisons shown, where mean values sharing the same letter are not significantly different within each occasion comparison.

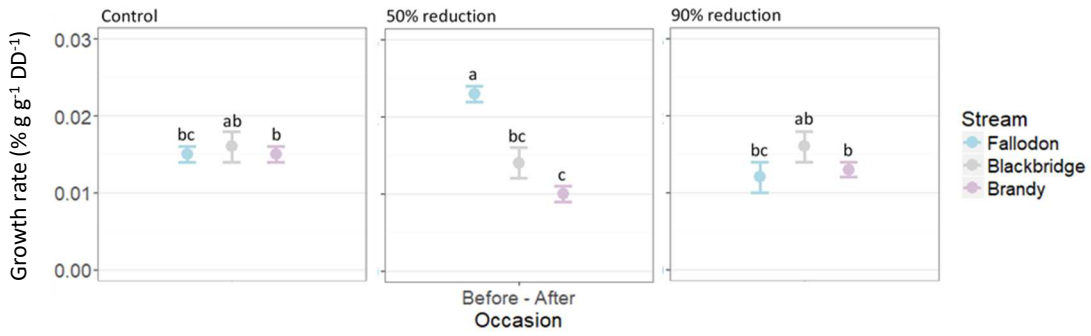

Figure 5.5: Influence of stream and experimental discharge reduction on mean (± standard error) growth rate of 1+ trout (% g g^{-1} DD^{-1}), showing lasting effects of the three different discharge treatments. Results of Tukey's post hoc comparisons shown, where mean values sharing the same letter are not significantly different.

5.3.4 ≥2+ trout

Similar to salmon and 0+ trout, there were no detectable effects of the discharge reduction on the growth rate of ≥2+ trout (Table 5.1), nor any difference in the response among streams (Table 5.2). There were also no detectable effects of experimental discharge reduction, or any lasting effects, on mean length and condition of ≥2+ trout within treatments across occasions (Table 5.3 & Table 5.4).

There were significant lasting effects of reduced discharge on the mean mass of ≥2+ trout (Table 5.4). Tukey's post hoc tests identified that the mean mass of ≥2+ trout within the 50% reduction treatment was significantly lower in the After occasion compared with the Before (Figure 5.6), whereas mean mass of ≥2+ trout within the

Control treatment and 90% reduction treatment was not significantly different to Before.

Between the Before and After sampling occasions, there were slightly elevated levels of loss in ≥2+ trout in all three streams as a result of 90% discharge reduction (Figure 5.7), which was not apparent for other species/cohorts. Within Brandy Stream, During the 90% discharge reduction 31.1% of ≥2+ trout moved out of the experimental area compared with 1.6% during the control treatment (Table 5.5).

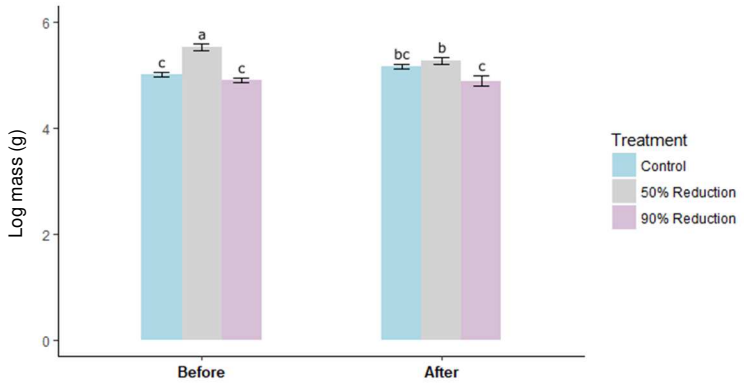

Figure 5.6: Lasting effects of experimental discharge reduction treatments on (log) mean (±standard error) mass of ≥2+ trout. Results of Tukey's post hoc comparisons shown: mean values sharing the same letter are not significantly different.

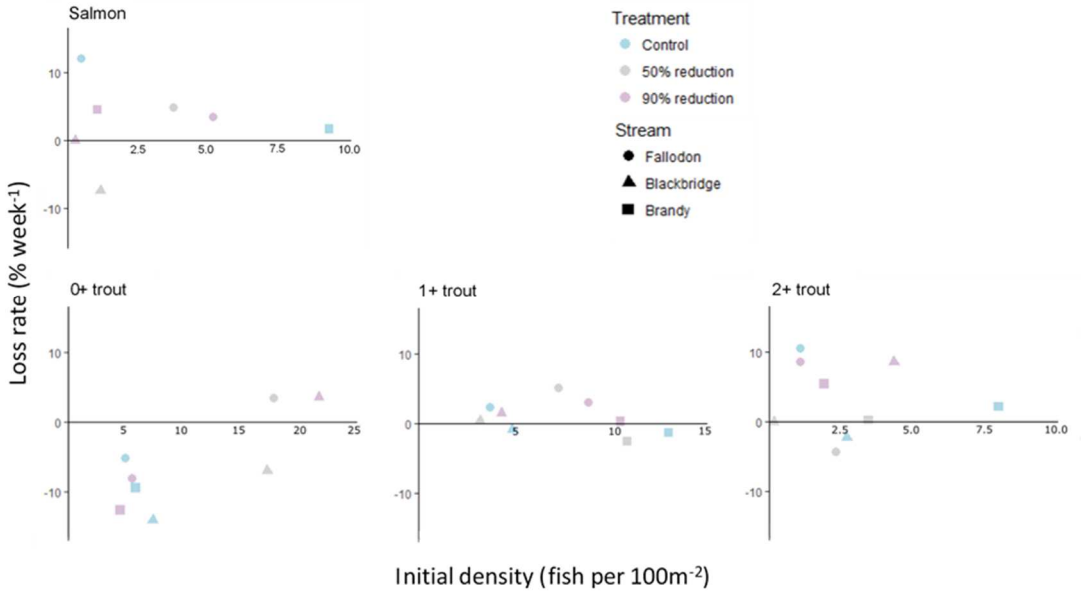

Figure 5.7: Loss rate (% week^{-1}) plotted against initial (Before) population density (fish per 100m^2) for salmon and trout cohort combinations when either a control, 50% and 90% discharge reduction was applied to each of the three study streams. All large negative loss rates (i.e. apparent increases in population) under very low Before densities have been omitted for clarity.

5.3.5 Estimated population size and salmonid density

The relative change in the total population of salmonids between the Before and After sampling occasions was not affected by the experimental manipulation of discharge (Treatment: $F_{(2,24)} = 2.02$, $p > 0.05$; Treatment:Cohort: $F_{(6,24)} = 0.35$, $p > 0.05$).

Salmonid species/cohort density varied between treatments and streams (Table A4.3). Across all streams there was generally a decrease in salmonid density after a 90% discharge reduction, which was not apparent in the Control. However, there was no significant effect of discharge manipulation on the relative change in salmonid density between the Before and After occasions (Treatment: $F_{(2,24)} = 2.07$, $p > 0.05$; Treatment:Cohort$_{(6,24)} = 0.49$, $p > 0.05$).

5.3.6 Growth rate of PIT tagged individuals caught across all thee sampling occasions

There were no detectable experimental effects, i.e. Treatment:Occasion and Treatment:Occasion:Stream, on the growth rate of PIT tagged individuals that were caught on all three sampling occasions (Table A4.4 & A4.5). However, as a

consequence of the small number of individuals that were caught the statistical power of this test was low and there was high variation in growth rate among individuals.

5.3.7 Differences amongst streams in salmonid mean length, mass and condition

Generally, the effects of discharge reduction on mean length, mass and condition indicated significant differences among streams between treatments across occasions for all species/cohort combinations (Table 5.6 & Table A4.6). However, Tukey's post hoc results were inconsistent and did not vary among streams in a manner that were related to the extent of stream physical change due to discharge reduction. For example: there were no significant differences in change over time amongst streams but there where trivial differences between Blackbridge Before as control and Brandy After as control (see Figure A4.3).

5.4 Discussion

Despite imposition of an extreme reduction of discharge in the current investigation, there were no negative effects on the growth rate of salmonids. This is a surprising result given that others report that reduced discharge negatively effects salmonid growth (Harvey *et al*., 2006; VerWey *et al*., 2018). Bacon *et al*. (2005) reported that the two main controls on salmonid growth are prey availability and water temperature. Streams with high base flows, i.e. chalk streams, are highly productive, and the discharge reduction did not reduce the density of benthic prey or the delivery of drifting prey in the study streams (Chapter 2 & 3). Furthermore, the water temperature, although raised and more variable, remained within the thermal limits for salmonid growth (Chapter 2; Jonsson & Jonsson, 2009). High productivity and stability of chalk stream conditions allows for quicker accumulation of body condition resulting in fish that are less vulnerable to discharge variations, unlike fish which live in cooler and less productive streams (Mann *et al*., 1989). Salmonids within the study streams also displayed high dietary plasticity (Chapter 3) and altered habitat use in response to discharge reduction (e.g. salmon and 0+ trout were located within relatively shallower water; Chapter 4) indicating that they can change their behaviour accordingly to ameliorate effects of reduced discharge.

Where any effects of discharge reduction on growth rate were detected they were positive. Growth rates of 1+ trout during the 50% reduction were significantly higher than the control and 90% reduction treatments. During the 50% reduction, 1+ trout had a higher proportion of terrestrial biomass in their guts and reduced gut prey abundance whilst consumption rates were maintained (Chapter 3). This suggests that 1+ trout were in profitable habitats (Chapter 4) maintaining a feeding position that allowed higher growth rates to be achieved as a result of selecting terrestrial prey, which were generally larger and, therefore, of greater nutritional value than aquatic prey (Fausch, 1984; Sotiropoulos *et al*., 2006; Davidson *et al*., 2010).

Along with growth rate, fish condition can be used as a measure of habitat quality for salmonids (Brodeur *et al*., 2004). In this experiment, mean salmon condition was unaltered following both discharge reduction treatments but declined within the control treatment. Reduced condition within the control treatment is in agreement with VerWey *et al*. (2018) who reported that salmonid condition decreased over the summer season. Unaltered mean condition of salmon following discharge reduction suggests that reduced discharge affected the normal summer development of salmon. In addition, following discharge re-instatement salmon guts contained an increased abundance and biomass of prey compared with before the reduction (Chapter 3), which may have allowed greater reserve tissue to be accumulated, resulting in a consistent condition over time (Rosenfeld & Boss, 2001; Bacon *et al*., 2005), compared with the control treatment. Following discharge reinstatement, salmon that experienced the reduction treatments would have had a greater mass due to fuller guts (Chapter 3) and would have been given a higher condition factor. However, fuller guts may be indicative of them playing catch up if we assume that they were struggling during reduced discharge conditions as increased emigration from the Brandy stream during 90% reduction might indicate.

Under reduced discharge conditions, individuals, particularly juveniles, of slow growth and low condition are likely to be lost first from a population (Macnaughton *et al*., 2015; Rosenfield, 2017). Loss of such individuals may occur if fish fail to adapt to reduced discharge conditions, or if such conditions create an environment which increases their vulnerability to predation (Lytle & Poff, 2004). In the current

investigation, we report that, over the three experimental years, weekly loss rates of salmon and 0+ trout within the study streams were within range of the long-term average of c. 10% per week (see Riley *et al*., 2009a), despite elevated levels of piscivory under experimental discharge reductions (Chapter 3). In addition to mortality (via reduced fitness and predation), loss of individuals from a population can also occur by movement out of the stream. Salmon increased movement out of Brandy stream during a 90% discharge reduction compared to the control, and discharge reinstatement resulted in some movement back into Brandy stream. Increased migration had no obvious effect on salmon weekly loss rates, unlike for ≥2+ trout.

Elevated loss of ≥2+ trout in the 90% reduction treatment, was observed in all streams. Elliott *et al*. (1997) reported that drought related mortality was higher in older cohorts in Brows Beck, the Lake District. However, elevated rates of loss of ≥2+ trout during reduced discharge could also be caused by increased movement out of the stream, as there is a limit as to how far territories can be compressed. Older (≥2+) trout showed increased movement (Chapter 4), as larger individuals may move greater distances to seek suitable habitats relative to smaller individuals (Young, 1994; Bunnell *et al*., 1998). Such directed movements demonstrate that older trout might seek to avoid the impacts of reduced discharge conditions through modification of behaviour (Nislow & Armstrong, 2012). In addition, smaller fish (such as juvenile salmon) may have been displaced by larger individuals (Kahler *et al*., 2001) and forced out of the experimental areas and over the SPD antennae. Inter-cohort competition is particularly high between salmonids (Nordwall *et al*., 2001; Einum & Kvingedal, 2011). Results from Brandy stream suggest that movement of ≥2+ trout out of the experimental area increased under the 90% discharge reduction. If this result was apparent across all study streams, then it may have enabled 1+ trout to increase their dominance within the streams and occupy larger and more favourable areas/territories once pre-manipulation discharge had been reinstated (Chapter 4), thus giving them an opportunity to occupy areas that allowed them to maintain consumption rate by consuming fewer, but larger prey items (Chapter 3).

A 50% discharge reduction within the Brandy stream resulted in no movement of salmon or 0+ trout in or out of the study stream. Reduced discharge has been

reported to hinder salmonid movement due to decreased longitudinal connectivity creating impassable barriers (Kahler *et al*., 2001; VerWey *et al*., 2018). However, as longitudinal connectivity was maintained under all treatments in the current investigation, it is likely discharge had not been reduced enough to trigger movement out of the stream as it was clear that individuals had high site loyalty during a 50% discharge reduction (Chapter 4). Perhaps when exposed to a 50% discharge reduction it was preferable for salmon and 0+ trout to remain in known habitat areas, indicating that competition for resources was low, unlike that observed under the 90% discharge reduction.

Recruitment, mortality and migration are the key variables that control salmonid population size (Phang *et al*., 2016). With the potential increase in movement out of the study streams during discharge reduction but no effect on the estimated population size it is likely that some individuals were a) missed in the Before fishing survey due to their small body size, b) untagged fish moving into the study site from much further downstream (Cold stream; see Figure 5.1), or c) numbers moving were smaller than the uncertainty around the estimates. At lower starting densities, there was often an apparent increase in abundance, resulting in negative loss rates for salmon and 0+ trout, possibly due to fish being missed during the Before fishing survey. One of the main disadvantages of using as a method to quantify fish numbers is the relatively low efficiency at capturing smaller individuals (Copp, 1989; Hedger *et al*., 2018).

It is widely accepted that under reduced discharge conditions fish density will increase initially as a result of reduced wetted width limiting the available habitat space (Kahler *et al*., 2001; Macnaughton *et al*., 2015). However, the long-term effects of discharge reduction on salmonid populations can vary due to natural density fluctuations between streams and years (Elliott *et al*., 1997; Kaylor *et al*., 2019). With the projected increase in severity of summer droughts, in the south of the UK, it is likely that reduced fish density following return to normal conditions in the current investigation, even though not significant, may be detrimental to the long-term productivity of salmonids in small chalk streams. In addition, it can be assumed that discharge reduction did not significantly increase avian and mammalian predation

within these streams as there was no long-term effects of discharge reduction on population size and density.

5.5 Conclusion

Overall there were no negative experimental effects of discharge reduction on salmonid growth nor on mean length, mass and condition (hypothesis 1). There was some evidence of movement out of the affected stream area (salmon and ≥2+ trout) during reduced discharge conditions (hypothesis 2), which increased the loss rate of ≥2+ trout (hypothesis 3). There were no significant negative effects of discharge reduction on salmonid population size and density (hypothesis 4). Overall the physical attributes of the individual streams did not result in consistent stream effects under reduced discharge conditions on salmonid growth (hypothesis 5).

There is a general consensus in the literature that reduced discharge will negatively impact the aquatic environment (Dudgeon *et al*., 2006; Jonsson & Jonsson, 2009; Rolls *et al*., 2012; Reid *et al*., 2019). This has put pressure on environmental agencies and fisheries managers for the restoration of impacted stream habitats, as well as water companies to ensure that enough water is left in rivers during times of low discharge. This study highlights that due to high salmonid dietary plasticity (Chapter 3) and a habitat utilisation response (Chapter 4) there are limited negative effects of reduced discharge on salmonid growth, migration and population size and density in chalk streams. This isn't to say that habitat monitoring and restoration measures should not persist, but if the right balance between habitat conservation (via bottom-up approaches) and discharge preservation can be met, chalk stream salmonids may prove highly resilient to short term summer reduced discharge conditions.

Chapter 6: Overall discussion

As a consequence of climate change and human alteration of the natural discharge regime in rivers (e.g. abstraction), low discharge events are likely to increase in both frequency and severity (Alcamo *et al*., 2007; Brown *et al*., 2013; Walters, 2016; Tonkin *et al*., 2019). To facilitate river managers and environmental agencies in mitigating detrimental impacts of low discharge events, a greater understanding of the response of river communities under such circumstances is needed. Therefore, replicated stream-scale experiments where discharge can be manipulated and the response of the riverine ecosystem (specifically physical characteristics, basal resources, macroinvertebrates and fish, and the various interactions among them) can be monitored and quantified is paramount.

Within this project, experimental reduction of discharge significantly reduced water depth, velocity and wetted width. However, on average, only 15% of wetted width was lost under the 90% reduction treatment indicating that, even though there was a break in lateral connectivity (e.g. established marginal habitats lost; Boulton, 2003; Lake, 2003), loss of wetted width was relatively small. In addition, longitudinal connectivity, even during the most severe discharge reduction treatment, was maintained. Channel morphology will have a marked effect on the response of rivers to discharge reduction. For example, in headwater streams in USA, discharge reduction of 97% resulted in a 52% reduction of riffle habitats and pools became the dominant flow type (Hakala & Hartman, 2004). As the chalk streams studied here lacked riffle pool sequencing, a characteristic typical of chalk streams (see Pretty *et al*., 2006) and other low gradient systems, it is perhaps not surprising that longitudinal connectivity was maintained. Alongside habitat quantity, habitat quality is an important ecosystem component (Walters, 2016). Increased stream temperatures are associated with reduced discharge events and can influence habitat quality for river communities (Cowx *et al*., 1984; Elliott, 2000). Within this project, although actual temperature differences were small (0.1 °C) discharge reduction increased longitudinal stream temperature differences (mean and range, see Figure 2.4) as sensible heat transfer (transfer of heat between the air and water) was enhanced over the imposed month-

long drought. White *et al*. (2017) report that rivers experiencing discharge reductions, as a result of river regulation, were on average 1.2 °C – 2.2 °C warmer than non-regulated rivers due to increased daily maximum temperatures. Increased temperature fluctuations as a result of reduced discharge treatments within this experiment were far smaller than those reported in mesocosms (Aspin *et al*., 2019a&b; Folegot *et al*., 2019), possibly due to the natural streams in this project having established riparian habitats, which can dampen temperature increases due to stream shading (Malcom *et al*., 2008; Hrachowitz *et al*., 2010). In addition, within this project water temperatures may not have increased as much as other studies as river discharge above the study stream sluice gates was not exposed to experimental discharge reduction. Here, stream discharge was the only variable that we manipulated, however, it is likely that in the future reduced discharge will be coupled with higher summer air temperatures (Murphy *et al*., 2009; NOAA, 2019a), which would further increase the temperature variation experienced (Hannah & Garner, 2015).

Previous studies have found that changes in physical characteristics associated with reductions in discharge are associated with increased availability of stream basal resources. The deposition of POM increases, as the carrying capacity of the water is reduced (Walters & Post, 2008), and entrapment by obstacles is greater (e.g. macrophytes, Kleeberg *et al*., 2010). Increases in periphyton occur as a result of elevated light penetration (due to reduced water depth) and increases in maximum water temperatures (Suren *et al*., 2003). However, in the current investigation, basal resources did not increase during experimental discharge reduction (see section 2.4.2 for detailed reasoning), therefore the physical habitat of the river-bed and resources were not substantially altered for macroinvertebrates.

During experimental discharge reduction macroinvertebrate density did not increase, which is surprising given the reduction in depth and wetted width would have reduced habitat availability. A 90% discharge reduction is a severe alteration to stream physical characteristics for organisms that are adapted to a relatively stable environment like chalk streams. In contrast, organisms within spate streams have presumably encountered more selection pressure to develop adaptations to variations

in discharge (Poff, 1992; McGuigan *et al*., 2003; Lytle & Poff, 2004; Lytle, 2008). Perhaps macroinvertebrates responded in a different way that went undetected, for example some macroinvertebrates may have drifted when reduced discharge was initiated or maybe there were few macroinvertebrates residing at the stream margins so a 15% reduction in wetted width may not have significantly increased density. It is also possible that macroinvertebrates have mechanisms that enable them to resist the impacts of reduced discharge such as utilisation of the hyporheic zone. Utilisation of the hyporheic zone can maintain community composition (Wood *et al.*, 2010), which may go some way in explaining why seasonal changes (occasion) had more pronounced effects on the macroinvertebrate assemblages than reduced discharge. Benthic macroinvertebrates constitute a large part of salmonid diet (White & Gowan, 2014). Lack of substantial change in the benthic macroinvertebrate assemblages, as well as their drift rate, as a result of reduced discharge suggest that salmonid prey availability remained unaltered over the experimental period.

As a result of no detectable effects of reduced discharge on prey availability salmonid gut content (abundance, richness, total biomass and proportion of terrestrial biomass) was not substantially affected by discharge reduction and only certain aspects of salmonid diet were influenced. For example, consumption rate of biomass for 0+ trout was maintained within the reduction treatments but decreased within the control, indicating that discharge reduction facilitated the consumption of larger prey items as there was no change in the consumption rate of individuals. This change in feeding behaviour may have limited any effects of discharge reduction, e.g. reduced growth rate, as salmonid diet displayed a high level of plasticity. Older salmonids eat larger prey items and a number of studies have reported that they become predominantly piscivorous at c.30 cm to maintain growth and condition (Steingrímsson & Gíslason, 2002; Hyvärinen & Huusko, 2006; Nunn *et al*., 2012). Here we report that experimental discharge reduction increased piscivory in ≥2+ trout and there was no associated change in growth rate or condition. Reduced discharge can increase fish density by a reduction in habitat availability (Kahler *et al*., 2001; Macnaughton *et al*., 2015) increasing encounter rates between individuals.

Reduced habitat availability, and corresponding increases in fish density and encounter rates, can alter fish habitat use and increase movements under discharge reductions (Riley *et al*., 2009a). Within the current investigation salmon and 0+ trout displayed reduced home stone loyalty during the 90% discharge reduction compared with the control treatment. Salmon and 0+ trout occupied relatively shallower water during the 90% discharge reduction compared with before. During drought, where there is increased competition for space and preferential feeding habitats, older dominant cohorts force smaller individuals into shallow peripheral stream areas (Kahler *et al*., 2001). The behaviour of older salmonids was also found to be influenced by discharge reduction as directed movement out of Brandy Stream, took place during the 90% discharge reduction, indicating that they actively seek to avoid negative impacts of the discharge reduction (Nislow & Armstrong, 2012). Riley *et al*. (2009a) concluded that reduced discharge of c. 90% had no effect on juvenile salmonid movement out of Brandy Stream, however this investigation reports that salmon increased movement out of the study area during the 90% discharge reduction. Smaller fish (such as juvenile salmon) may have been displaced and forced out of the experimental areas by larger dominant individuals. Overall, effects of discharge reduction on salmonid habitat use and movement were transient and had few lasting effects.

Growth rate of 1+ trout increased during discharge reduction in this study. This might have been caused by competitive release from older dominant individuals and increased available habitat. Experimental field studies report that the presence of older age classes negatively influence the growth of younger individuals (Nordwall *et al*., 2001; Kaspersson & Hojesjo, 2009). Thus, movement of ≥2+ trout out of the affected stream area during 90% discharge reduction may have had a positive effect on 1+ trout growth. However, this is assuming that movement patterns within Brandy Stream is also replicated across Fallodon Stream and Blackbridge Stream, which is plausible as there was a higher loss rate of ≥2+ trout during 90% discharge reduction in all streams (Figure 5.7).

Despite some reshuffling of diet, habitat use and small-scale movement under reduced discharge conditions, younger salmonids (in particular 0+ and 1+ trout) appear

to deploy a 'sit it out' strategy. Long distance search for new habitat/territory would increase predation risk and involve competing for new territories (Bond *et al*., 2008), so perhaps it is more beneficial for fish of this size to remain in known habitats and defend their established territories. There were no significant lasting effects of discharge reduction on population size and density, which is not surprising given the plasticity and resilience displayed by salmon and trout within these streams. Specifically, there were no lasting effects of experimental discharge reduction on site loyalty, suggesting that salmonids, within these streams, have high resilience and site fidelity despite extreme reductions in discharge. Jones & Petreman (2013) also report that, across 30 lowland streams in Canada, low discharge events had no overall impact on fish density, but salmonid growth rates were reduced as a result of increased water temperatures. Water temperature is considered to be one of the most important factors that determines growth rates, habitat use and movement (Graham & Harrod, 2009). Within this study longitudinal temperature differences varied with treatment (0.4 °C during the 90% reduction treatment, 0.3 °C during the 50% reduction treatment and 0.2 °C in the control). Perhaps the increased temperatures (mean and range) during the discharge reduction treatments in this study were too small to initiate an overall directional response of salmonids to reduced discharge conditions.

This project was unique as it investigated the potential bottom up controls of reduced discharge on salmonid ecosystems, going one step further than Riley *et al*., (2009a) who investigated only the direct impacts of reduced discharge on salmonid habitat use, movement and mortality in Brandy stream. Although potential bottom up controls were investigated, it can be concluded that within these streams, discharge reduction seemed to have direct effects (via changes in physical characteristics) on salmonids rather than indirect effects (via changes in basal resources and macroinvertebrates [prey availability]; see Figure 6.1).

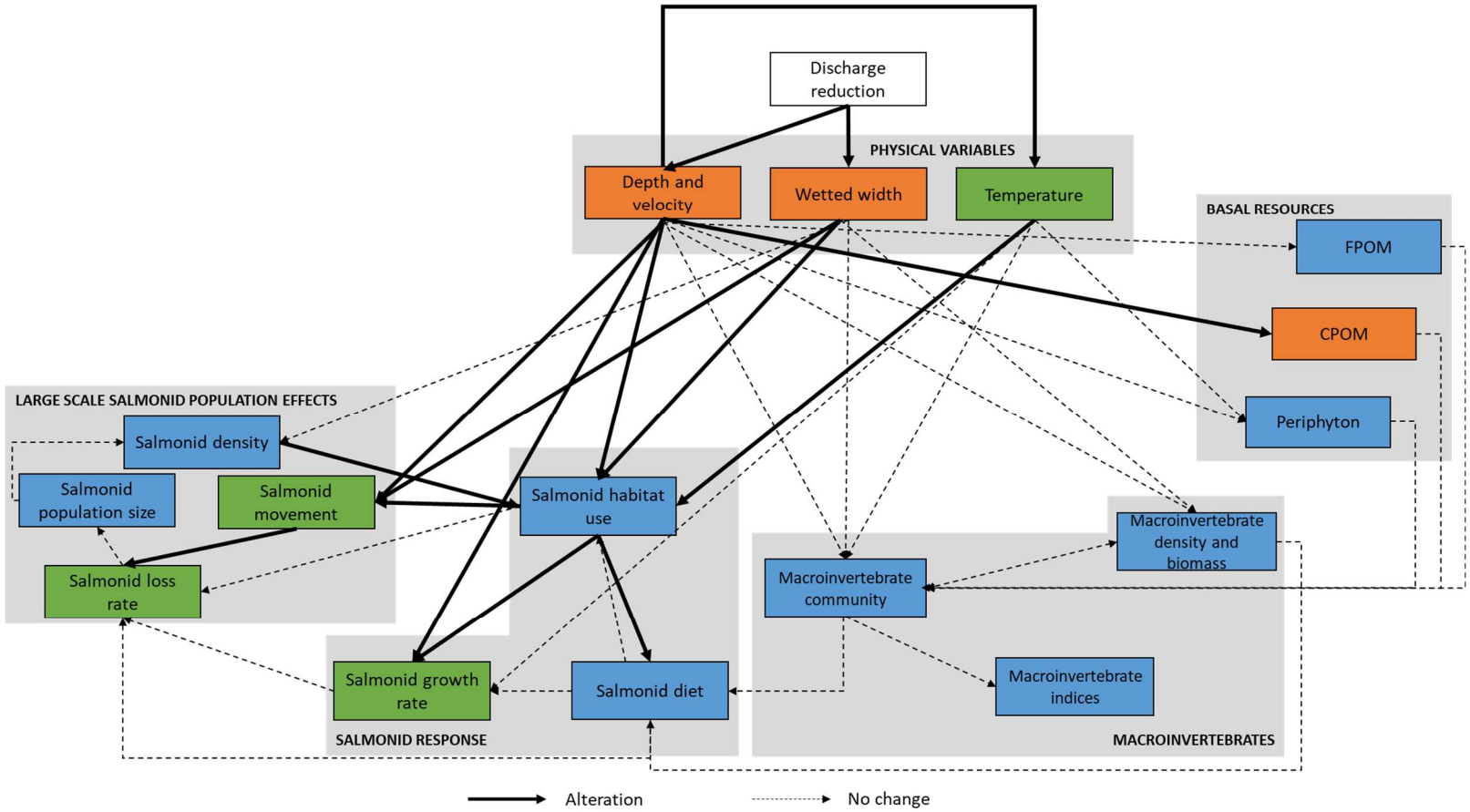

Figure 6.1: Summary of the effects that experimental discharge reduction had on salmonid ecosystems within this study. Links based on hypothesis within Table 1.1. Coloured boxes indicate increase (green), decrease (orange) and no-directional change (blue) as a result of experimental discharge reduction.

Whilst stream-scale experiments are important to fully understand biological interactions, experimental designs are confounded by the natural layout of rivers; therefore, replication of streams is generally low. For example, Milner *et al*. (2018) investigated the effects of extreme hydrological events on river ecosystem resilience but only sampled one river. Therefore, mesocosms have been popular for studying extreme discharge conditions as, despite reduced realism, replication of experimental treatments is relatively easy (Woodward *et al*., 2010; Stewart *et al*., 2013). Some examples include Aspin *et al*. (2019a&b) who used 21 stainless steel channels to study the effects of drought intensification on invertebrate assemblages and Ledger *et al*. (2012) who used 4 mesocosm blocks with 3 linear channels in each block to study the effects of climate change on community resilience. Using natural systems and studying populations of wild animals (in this case salmonids), sample size is restricted to the number of individuals present at the time of sampling. Within this project salmon abundances were low in all three streams, so 0+ and 1+ cohorts were grouped in order to provide greater power to statistical tests to detect differences. However, as salmon sample size was still low compared with trout cohorts, small experimental effects were less likely to be detected (Krzywinski & Altman, 2013). Despite limitations, results from this study suggest that salmonids, within these chalk streams, are highly resilient to reduced discharge conditions, which is particularly surprising as chalk streams have a very stable discharge regime which is reflected by the communities within them (Mann *et al*., 1989; Berrie, 1992; Prenda *et al*., 1997).

Under laboratory conditions fish show a strong movement response to reduced discharge (Kraft, 1972; Davey *et al*., 2006). However, due to the structural complexity of streams the impacts of reduced discharge and salmonid ecosystems are not clear cut, and management strategies based on the results of artificial experiments (not stream-scale) should be implemented with caution. Compared with artificial experiments, many stream-scale experiments are opportunistic and as a result rarely encompass sampling that enables understanding of the mechanisms for how reduced discharge reduction may affect the riverine ecosystem. For example, upon studying the effects of a mega-drought on macroinvertebrates and fish communities in California, McDevitt-Galles & Johnson (2018) commenced sampling once the drought had already

started and sampling stopped before drought had ended. If adequate baseline data or data collected after the event is missing it is hard to attribute cause and effect (Ledger *et al*., 2013). Here we were able to plan a stream-scale experiment that allowed for sufficient baseline data to be collected, in addition to sampling once pre-manipulation discharge had been re-instated, which enabled a greater understanding of the mechanisms underlining the effects of reduced discharge (Worrall *et al*., 2014). These mechanistic results were then able to help determine why such processes may become evident during discharge reduction.

Tonkin *et al*. (2019) report that process-based models are important in the future management of fisheries. However, they are seldom used, as such data are costly to collect. This study provides valuable data that could be used in such models to help guide future management in chalk streams. This information can help validate hydro-ecology models, such as the widely used physical habitat simulation system (PHABSIM), which will allow them to be applied with greater confidence (Rosenfeld, 2017). As well as model validation, results of this project can help underpin resilience-based management plans that are becoming increasingly important due to the rapidly changing environment (Carlson *et al*., 2017). Such models can help prioritise, implement and adapt management actions to help sustain salmonid ecosystems threatened by low river discharge. If the duration of reduced discharge is in the order of a month and within this time lateral, and longitudinal, hydrological connectivity is maintained, the best management practise may be to leave fish where they are. However, if connectivity is lost fisheries managers may have to consider fish rescues. Nevertheless, it is debatable whether the stress and consequent mortality involved with such operations and the additional stress caused when establishing new territories (which would also impact resident fish where the rescued fish were relocated to) is less than that experienced if fish remained in the stream (Riley *et al*., 2009a).

Some of the priority issues currently facing managers of the River Itchen catchment is reduced discharge, along with water quality and channel structure and function (Environment Agency, 2015). The Environment agency plans to maintain and enhance channel habitats to help them become more resilient of reduced discharge.

This project can be used as an example of where natural variations in channel form, along with high habitat heterogeneity may be enough to help migratory and resident salmonids persist under short to medium term extreme drought conditions. In addition, further work that might help agencies understand how to enhance chalk stream resilience, could be to study the effects of long-term reduced discharge (mimicking a supra-seasonal drought). Within the experimental system set up on the River Itchen, streams could be monitored effectively and provide valuable information on how the communities within them alter as the drought perpetuates. Encompassed within this would be continued monitoring once pre-experimental discharge conditions have been re-instated, which would enable managers to establish how chalk streams recover after such an event and how long it takes them to potentially return to a pre-drought state. Other possible avenues of further study include: a) initiating low discharge as a ramp disturbance rather than a press, as it is more likely that drought conditions will develop over time (Lake, 2003), and b) investigating the effects of increased winter discharge as it is likely that, as a result of climate change, rainfall during winter months is going to increase in the south of the UK (Murphy *et al*., 2009), which could result in higher base flows and further influence salmonid populations.

By utilising long term data sets some studies have tried to identify key aspects of the river discharge and the influence it has on salmonid densities (e.g. Grossman *et al*. 2017; Honkanen *et al*., 2018). Fabris *et al*. (2019) investigated discharge variations on salmon densities within an upland Scottish river. They concluded that low discharge events, interspersed with high stream discharge events, are the most detrimental to salmon densities with summer being the most sensitive period. There findings are in slight contrast with Gillson *et al*. (in review) where it is reported that, within the salmon index rivers in England and Wales (including a chalk stream – River Frome), high discharges have a greater impact on parr communities compared to low discharges. Results from the current small-scale study are in line with other larger-scale studies on chalk rivers, indicating that the findings of this project may provide highly useful information when explaining the mechanisms of why large-scale results occur.

It is important to remember that, within this study, stream discharge was supplied at a constant rate when the experiment was not taking place and the surrounding land use was a nature reserve. As a result, perhaps to a certain extent, the study streams are not a true reflection of UK chalk streams and the year round pressures they face. One example of a year-round pressure is water abstraction. UK chalk rivers, such as the River Itchen, are heavily abstracted from due to societal demands (Cox & Ozdemiroglu, 2018). Thus, the aquatic community within these rivers may have different resistance and resilience thresholds when atypical, reduced summer discharge occurs compared to the study streams. In addition, UK chalk streams occur within catchments heavily dominated by agriculture. Reduced water quality as a result of increased sediment inputs and nutrient run-off from farming practices can impact river communities (Davis *et al*., 2018).

Alongside these pressures, climate change will continue to have a stronger impact on seasonal weather. Atypical summer droughts will become more typical and new stresses on the riverine ecosystem will start to manifest. Species distribution of non-native species will start to proliferate in areas that were previously unfavourable. Although not at the study sites, American signal cray fish are present in the River Itchen headwaters (Robinson *et al*., 2018). Signal crayfish are highly destructive burrowers, they have the ability to alter the riverbed profile (impacting the wetted width of a stream during drought) and increase sediment loads (Sanders *et al*., 2018). Where signal cray fish are present, Galib (2020) reported that benthic fish abundance and young of the year salmonids decreased and the opposite was recorded in uninvaded streams. Galib (2020) also reported a dramatic decline in macroinvertebrate abundance and taxonomic richness in invaded streams. In addition, signal crayfish are also voracious grazers compared to the native white clawed crayfish (Nystrom & Strand, 1996). Reduced macrophyte abundance can reduce stream water retention in the summer, lower initial summer depths coupled with reduced discharge events will collectively have a greater impact on the freshwater ecosystem. Overall, pressures mentioned above, plus others, will have accumulative effects and alter stream community resistance and resilience to reduce discharge events. Over time

macroinvertebrate composition will be drastically altered and a new, more resilient community will be present.

Although the potential outlook for chalk streams is bleak, pressures mentioned are reversable/preventable/manageable. If we (scientists/policy makers/water companies/public), work together we can reduce the impact that we have on these streams and the pressures that they are under. The results of this study provide an important positive message: chalk stream resilience to reduced summer discharge is high if background pressure is low. Now is the time for us to act, increase chalk stream resilience and help safeguard our chalk streams that are quintessential to the British landscape.

6.1 Thesis conclusion

Future predictions are that salmonid populations within the UK are going to decline as a result of summer climate change (Graham & Harrod, 2009). The overall aim of this work was to determine the impact of reduced summer discharge, as a result of climate change and human impacts, on chalk stream salmonid ecosystems. Despite some re-shuffling at each level (basal, macroinvertebrates and fish) overall, salmonids within these streams displayed high levels of resilience to reduced discharge conditions. These high levels of resilience may be attributable to two main factors: 1) limited loss of wetted width even under the most severe discharge reduction treatment, and 2) lack of a response by basal resource and macroinvertebrates (fish prey) to reduced discharge. It appears that, with the right management strategies, supported by the findings of this project, migratory and resident populations of salmonids within chalk streams may be able to persist even during the most extreme discharge reductions.

References

Aadland L.P. (1993) Stream habitat types: their fish assemblages and relationship to flow, *North American Journal of Fisheries Management*, *13*(4), 790-806.

Acreman M., Dunbar M., Hannaford J., Mountford O., Wood P., Holmes N., Cowx I., Noble R., Extence C., Aldrick J. & King J. (2008) Developing environmental standards for abstractions from UK rivers to implement the EU Water Framework, *Hydrological Sciences Journal*, *53*(6), 1105-1120.

Acreman M.C. & Dunbar M.J. (2010) *Ecologically acceptable flows in chalk rivers*, Environment Agency, UK.

Acuña V., Giorgi A., Muñoz I., Uehlinger U.R.S. & Sabater S. (2004) Flow extremes and benthic organic matter shape the metabolism of a headwater Mediterranean stream, *Freshwater Biology*, *49*(7), 960-971.

Acuña V., Muñoz I., Giorgi A., Omella M., Sabater F. & Sabater S. (2005) Drought and postdrought recovery cycles in an intermittent Mediterranean stream: structural and functional aspects, *Journal of the North American Benthological Society*, *24*, 919-933.

Agrawal A.A. (2001) Phenotypic plasticity in the interactions and evolution of species, *Science*, *294*, 321-326.

Alberts J.M., Fritz K.M. & Buffam I. (2018) Response to basal resources by stream macroinvertebrates is shaped by watershed urbanization, riparian canopy cover, and season, *Freshwater Science*, *37*(3), 640-652.

Alcamo J., Flörke M. & Märker M. (2007) Future long-term changes in global water resources driven by socio-economic and climatic changes, *Hydrological Sciences Journal*, *52*(2), 247-275.

Anderson C. & Cabana G. (2007) Estimating the trophic position of aquatic consumers in river food webs using stable nitrogen isotopes Estimating the trophic position of aquatic consumers in river food webs using stable nitrogen isotopes, *Journal of the North American Benthological Society*, *26*(2), 273-285.

Armitage P.D., Moss D., Wright J.F. & Furse M.T. (1983) The performance of a new biological water quality score system based on macroinvertebrates over a wide range of unpolluted running-water sites, *Water research*, *17*(3), 333-347.

Armstrong J.D., Braithwaite V.A. & Rycroft P. (1996) A flat-bed passive integrated transponder antenna array for monitoring behaviour of Atlantic salmon parr and other fish, *Journal of Fish Biology*, *48*, 539-541.

Armstrong J.D., Braithwaite V.A. & Fox M. (1998) The response of wild Atlantic salmon parr to acute reductions in water flow, *Journal of Animal Ecology*, *67*(2), 292-297.

Armstrong J.D., Kemp P.S., Kennedy G.J.A., Ladle M. & Milner N.J. (2003) Habitat requirements of Atlantic salmon and brown trout in rivers and streams, *Fisheries research*, *62*(2), 143-170.

Arroita M., Flores L., Larrañaga A., Martínez A., Martínez-Santos M., Pereda O., Ruiz-Romera E., Solagaistua L. & Elosegi A. (2017) Water abstraction impacts stream ecosystem functioning via wetted-channel contraction, *Freshwater Biology*, *62*(2), 243-257.

Arthington A.H., Kennen J.G., Stein E.D. & Webb J.A. (2018) Recent advances in environmental flows science and water management—Innovation in the Anthropocene, *Freshwater biology*, *63*(8), 1022-1034.

Aspin T.W., Khamis K., Matthews T.J., Milner A.M., O'callaghan M.J., Trimmer M., Woodward G. & Ledger M.E. (2019a) Extreme drought pushes stream invertebrate communities over functional thresholds, *Global Change Biology*, *25*(1), 230-244.

Aspin T.W., Hart K., Khamis K., Milner A.M., O'Callaghan M.J., Trimmer M., Wang Z., Williams G.M., Woodward G. & Ledger M.E. (2019b) Drought intensification alters the composition, body size, and trophic structure of invertebrate assemblages in a stream mesocosm experiment, *Freshwater Biology*, *64*(4), 750-760.

Ayllón D., Almodóvar A., Nicola G.G. & Elvira B. (2009) Interactive effects of cover and hydraulics on brown trout habitat selection patterns, *River Research and Applications*, *25*(8), 1051-1065.

Ayllón D., Almodóvar A., Nicola G.G. & Elvira B. (2012) The influence of variable habitat suitability criteria on PHABSIM habitat index results, *River Research and Applications*, *28*(8), 1179-1188.

Bacon P.J., Gurney W.S.C., Jones W., McLaren I.S. & Youngson A.F. (2005) Seasonal growth patterns of wild juvenile fish: partitioning variation among explanatory variables, based on individual growth trajectories of Atlantic salmon (*Salmo salar*) parr, *Journal of Animal Ecology*, *74*(1), 1-11.

Baird O.E & Krueger CC. (2003) Behavioral thermoregulation of Brook and Rainbow Trout: Comparison of summer habitat use in an Adirondack river, New York, *Transactions of the American Fisheries Society*,*132*, 1194-1206.

Baker E.A. & Coon T.G. (1997) Development of evaluation criteria of alternative habitat suitability criteria for brook trout, *Transactions of the American Fisheries Society*, *126*, 65-76.

Bal K. & Meire P. (2009) The influence of macrophyte cutting on the hydraulic resistance of lowland rivers, *Journal of Aquatic Plant Management*, *47*, 65–68.

Bardonnet A. & Baglinière J.L. (2000) Freshwater habitat of Atlantic salmon (*Salmo salar*), *Canadian Journal of Fisheries and Aquatic Sciences*, *57*(2), 497-506.

Baxter C.V., Fausch K.D. & Saunders W.C (2005) Tangled webs: reciprocal flows of invertebrate prey link streams and riparian zones, *Freshwater Biology*, *50*(2), 201-220.

Beach M.H. (1984) *Fish Pass Design – Criteria for the Design and Approval of Fish Passes and Other Structures to Facilitate the Passage of Migratory Fish in Rivers*, Fisheries Research Technical Report No. 78. Directorate of Fisheries Research, Ministry of Agriculture, Fisheries and Food, Lowestoft, UK.

Bear E.A., McMahon T.E. & Zale A.V. (2007) Comparative thermal requirements of Westslope Cutthroat Trout and Rainbow Trout: implications for species interactions and development of thermal protection standards, *Transactions of the American Fisheries Society*, *136*, 1113-1121.

Beecher H.A., Caldwell B.A., DeMond S.B., Seiler D. & Boessow S.N. (2010) An empirical assessment of PHABSIM using long-term monitoring of coho salmon smolt production in Bingham Creek, Washington, *North American Journal of Fisheries Management*, *30*(6), 1529-1543.

Benejam L., Angermeier P.L., Munné A. & García-Berthou E. (2010) Assessing effects of water abstraction on fish assemblages in Mediterranean streams, *Freshwater Biology*, *55*, 628-642.

Benke A.C., Huryn A.D., Smock L.A. & Wallace J.B. (1999) Length-mass relationships for freshwater macroinvertebrates in North America with particular reference to the southeastern United States, *Journal of the North American Benthological Society*, *18*(3), 308-343.

Beresford A.L. & Jones J.I. (2010) Weedbeds and big bugs; towards a fuller understanding of the interactions between macrophytes, periphyton, plant associated invertebrates and fish, *Freshwater Biology, 55*, 514-530.

Berrie A.D. (1992) The chalk-stream environment, *Hydrobiologia*, *248*(1), 3-9.

Blunden J. & Arndt D.S. (2016) State of the Climate in 2015, *Bulletin of the American Meteorological Society*, *97*(8), Si-S275.

Bickerton M., Petts G., Armitage P. & Castella E. (1993) Assessing the ecological effects of groundwater abstraction on chalk streams: three examples from eastern England, *Regulated Rivers: Research & Management*, *8*(1-2), 121-134.

Biggs B.J. & Close M.E. (1989) Periphyton biomass dynamics in gravel bed rivers: the relative effects of flows and nutrients, *Freshwater Biology*, *22*(2), 209-231.

Birk S., Bonne W., Borja A., Brucet S., Courrat A., Poikane S., Solimini A., Van De Bund W., Zampoukas N. & Hering D. (2012) Three hundred ways to assess Europe's surface waters: An almost complete overview of biological methods to implement the Water Framework Directive, *Ecological Indicators*, *18*, 31-41.

Biro P.A., Abrahams M.V., Post J.R. & Parkinson E.A. (2006) Behavioural trade-offs between growth and mortality explain evolution of submaximal growth rates, *Journal of Animal Ecology*, *75*(5), 1165-1171.

Bo T., Fenoglio S., Malacarne G., Pessino M. & Sgariboldi F. (2007) Effects of clogging on stream macroinvertebrates: An experimental approach, *Limnologica*, *37*, 186-192.

Boersma K.S., Bogan M.T., Henrichs B.A. & Lytle D.A. (2014) Invertebrate assemblages of pools in arid-land streams have high functional redundancy and are resistant to severe drying, *Freshwater Biology*, *59*, 491–501.

Bohlin T., Hamrin S., Heggberget T.G., Rasmussen G. & Saltweit S.J. (1989) Electrofishing-Theory and practice with special emphasis on salmonids, *Hydrobiologia*, *173*, 9-43.

Bohlin T., Pettersson J. & Degerman E. (2001) Population density of migratory and resident brown trout (*Salmo trutta*) in relation to altitude: evidence for a migration cost, *Journal of Animal Ecology*, *70*(1), 112-121.

Bolnick D.I., Svanback R., Fordyce J.A., Yang L.H., Davis J.M., Hulsey C.D. & Forister M.L. (2003) The ecology of individuals: Incidence and implications of individual specialization, *American Naturalist*, *161*, 1-28.

Bond N.R., Lake P.S. & Arthington A.H. (2008) The impacts of drought on freshwater ecosystems: an Australian perspective, *Hydrobiologia*, *600*(1), 3-16.

Boulton A.J. (2003) Parallels and contrasts in the effects of drought on stream macroinvertebrate assemblages, *Freshwater Biology*, *48*(7), 1173-1185.

Bowles F.J. & Henderson P. (2012) Water resource management–the water utilities view, *Fisheries Management and Ecology*, *19*(6), 484-489.

Bridcut E.E. & Giller P.S. (1995) Diet variability and foraging strategies in brown trout (*Salmo trutta*): an analysis from subpopulations to individuals, *Canadian Journal of Fisheries and Aquatic Sciences*, *52*(12), 2543-2552.

Brodeur R.D., Fisher J.P., Teel D.J., Emmett R.L., Casillas E. & Miller T.W. (2004) Juvenile salmonid distribution, growth, condition, origin, and environmental and species associations in the Northern California Current, *Fishery Bulletin*, *102*(1), 24-46.

Brown T.C., Foti R & Ramírez J.A. (2013) Projected freshwater withdrawals in the United States under a changing climate, *Water Resources Research*, *49*, 1259-1276.

Bunn S.E. & Arthington A.H. (2002) Basic principles and ecological consequences of altered flow regimes for aquatic biodiversity, *Environmental Management*, *30*(4), 492-507.

Bunnell D.B., Isely J.J., Burrell K.H. & Van Lear D.H. (1998) Diel movement of Brown Trout in a southern Appalachian river, *Transactions of the American Fisheries Society*, *127*, 630-636.

Burgherr F. & Meyer E.I. (1997) Regression analysis of linear body dimensions vs. dry mass in stream macroinvertebrates, *Fundamental and Applied Limnology*, *139*, 101-112.

Butturini A., Guarch A., Romaní A.M., Freixa A., Amalfitano S., Fazi S. & Ejarque E. (2016) Hydrological conditions control in situ DOM retention and release along a Mediterranean river, *Water Research*, *99*, 33-45.

Caissie D. (2006) The thermal regime of rivers: a review, *Freshwater Biology*, *51*(8), 1389-1406.

Caldwell T.J., Rossi G.J., Henery R.E. & Chandra S. (2018) Decreased streamflow impacts fish movement and energetics through reductions to invertebrate drift body size and abundance, *River Research and Applications*, *34*(8), 965-976.

Carlson A.K., Taylor W.W., Schlee K.M., Zorn T.G. & Infante D.M. (2017) Projected impacts of climate change on stream salmonids with implications for resilience-based management, *Ecology of Freshwater Fish*, *26*(2), 190-204.

Chadd R.P., England J.A., Constable D., Dunbar M.J., Extence C.A., Leeming D.J., Murray-Bligh J.A. & Wood P.J. (2017) An index to track the ecological effects of drought development and recovery on riverine invertebrate communities, *Ecological Indicators*, *82*, 344-356.

Chessman B.C., Westhorpe D.P., Mitrovic S.M. & Hardwick L. (2009) Trophic linkages between periphyton and grazing macroinvertebrates in rivers with different levels of catchment development, *Hydrobiologia*, *625*(1), 135-150.

Clarke R., Davy-Bowker J., Dunbar M., Laize C., Scarlett P. & Murphy J. (2011) *Enhancement of the river invertebrate classification tool Final Report*, Project WFD119.

Coates S., Tanna P. & Scott-Allen E. (2019) *Overview of the UK population: August 2019*, Office for National Statistics.

Conallin J., Boegh E., Olsen M., Pedersen S., Dunbar M.J. & Jensen J.K. (2014) Daytime habitat selection for juvenile parr brown trout (*Salmo trutta*) in small lowland streams, *Knowledge and Management of Aquatic Ecosystems*, (413), 9.

Copp G.H. (1989) Electrofishing for fish larvae and 0+ juveniles: equipment modifications for increased efficiency with short fishes, *Aquaculture Research*, *20*(4), 453-462.

Cortes R.M.V., Ferreira M.T., Oliveira S.V. & Oliveira D. (2002) Macroinvertebrate community structure in a regulated river segment with different flow conditions, *River Research and Applications*, *18*(4), 367-382.

Cowx I.G., Young W.O. & Hellawell J.M. (1984) The influence of drought on the fish and invertebrate populations of an upland stream in Wales, *Freshwater Biology*, *14*, 165-177.

Cowx I.G. & Fraser D. (2003) *Monitoring the Atlantic Salmon*, Conserving Natura 2000 Rivers Monitoring Series No. 7, English Nature, Peterborough.

Cowx I.G., Harvey J.P., Noble R.A. & Nunn A.D. (2009) Establishing survey and monitoring protocols for the assessment of conservation status of fish populations in river Special Areas of Conservation in the UK, *Aquatic Conservation: Marine and Freshwater Ecosystems*, *19*(1), 96-103.

Cox J. & Ozdemiroglu E. (2018) Water Abstraction from the River Itchen, Hampshire, United Kingdom, *Equivalency Methods for Environmental Liability,* 235-267*,* Springer, Dordrecht.

Cuffney T.F. & Wallace J.B. (1989) Discharge-export relationships in headwater streams: the influence of invertebrate manipulations and drought, *Journal of the North American Benthological Society*, *8*(4), 331-341.

Daufresne M., Bady P. & Fruget J. (2007) Impacts of global changes and extreme hydroclimatic events on macroinvertebrate community structures in the French Rhone River, *Oecologia*, 151, 544-559.

Davey A.J.H., Kelly D.J. & Biggs B.J.F. (2006) Refuge-use strategies of stream fishes in response to extreme low flows, *Journal of Fish Biology*, *69*, 1047-1059.

Davey A.J.H. & Kelly D.J. (2007) Fish community responses to drying disturbances in an intermittent stream: a landscape perspective, *Freshwater Biology*, *52*(9), 1719-1733.

Davidson R.S., Letcher B.H. & Nislow K.H. (2010) Drivers of growth variation in juvenile Atlantic Salmon (*Salmo salar*): an elasticity analysis approach, *Journal of Animal Ecology*, *79*, 1113-1121.

Davies P.M., Naiman R.J., Warfe D.M., Pettit N.E., Arthington A.H. & Bunn S.E. (2014) Flow–ecology relationships: closing the loop on effective environmental flows, *Marine and Freshwater Research*, *65*(2), 133-141.

Davis S.J., Mellander P.E., Kelly A.M., Matthaei C.D., Piggott J.J. & Kelly-Quinn M. (2018) Multiple-stressor effects of sediment, phosphorus and nitrogen on stream macroinvertebrate communities, *Science of the Total Environment*, *637*, 577-587.

Defra (2011) Water for Life, UK.

Defra (2013) Making the most of every drop, Consultation on reforming the water abstraction management system, UK.

Defra (2017a) Water abstraction plan: Catchment focus, Policy paper, UK.

Defra (2017b) Water abstraction plan: Abstraction licensing service, Policy paper, UK.

Denis D. & Jiménez A. (2009) Weight-length regressions in aquatic prey of Cuban wading birds, *Journal of Caribbean Ornithology*, *22*(1), 32-36.

Descroix A., Desvilettes C., Martin P., Anneville O., Bec A. & Bourdier G. (2009) Feeding, growth and nutritional status of restocked salmon parr along the longitudinal gradient of a large European river: The Allier, *Ecology of Freshwater Fish*, *18*, 282-296.

Dewson Z.S., James A.B. & Death R.G. (2007a) Stream ecosystem functioning under reduced flow conditions, *Ecological Applications*, *17*(6), 1797-1808.

Dewson Z.S., James A.B. & Death R.G. (2007b) A review of the consequences of decreased flow for instream habitat and macroinvertebrates, *Journal of the North American Benthological Society*, *26*(3), 401-415.

Dill L.M. (1983) Adaptive flexibility in the foraging behavior of fishes, *Canadian Journal of Fisheries and Aquatic Sciences*, *40*(4), 398-408.

Dineen G., Harrison S.S.C. & Giller P.S. (2007) Diet partitioning in sympatric Atlantic salmon and brown trout in streams with contrasting riparian vegetation, *Journal of Fish Biology*, *71*(1),17-38.

Dinh Y.T. & Death R.G. (2018) Do disturbance and periphyton productivity affect stream invertebrate traits?, *Freshwater Science*, *37*(2), 367-379.

Dodrill M.J., Yackulic C.B., Kennedy T.A. & Hayes J.W. (2016) Prey size and availability limits maximum size of rainbow trout in a large tailwater: insights from a drift-foraging bioenergetics model, *Canadian Journal of Fisheries and Aquatic Sciences*, *73*(5), 759-772.

Doledec S., Forcellini M., Olivier J. & Roset N. (2015) Effects of large river restoration on currently used bioindicators and alternative metrics, *Freshwater Biology*, *60*, 1221-1236.

Dudgeon D., Arthington A.H., Gessner M.O., Kawabata Z.I., Knowler D.J., Lévêque C., Naiman R.J., Prieur-Richard A.H., Soto D., Stiassny M.L. & Sullivan C.A. (2006) Freshwater biodiversity: importance, threats, status and conservation challenges, *Biological Reviews*, *81*(2), 163-182.

Dugdale S.J., Franssen J., Corey E., Bergeron N.E., Lapointe M. & Cunjak R.A. (2016) Main stem movement of Atlantic salmon parr in response to high river temperature, *Ecology of Freshwater Fish*, *25*(3), 429-445.

Dunbar M.J., Pedersen M.L., Cadman D.A.N., Extence C., Waddingham J., Chadd R. & Larsen S.E. (2010) River discharge and local-scale physical habitat influence macroinvertebrate LIFE scores, *Freshwater Biology*, *55*(1), 226-242.

Durance I. & Ormerod S.J. (2009) Trends in water quality and discharge confound long-term warming effects on river macroinvertebrates, *Freshwater Biology*, *54*(2), 388-405.

Edwards C.A. (1998) *Earthworm ecology*, St. Lucie Press, New York.

Edwards F.K., Lauridsen R.B., Duerdoth C.P. & Jones J.I. (2008) Dry and ash-free dry mass to length relationships of bullhead (*Cottus gobio* L.), *Fundamental and Applied Limnology*, *172*(4), 315-316.

Edwards F.K., Lauridsen R.B., Armand L., Vincent H.M. & Jones J.I (2009) The relationship between length, mass and preservation time for three species of freshwater leeches (Hirudinea), *Fundamental and Applied Limnology*, *173*, 321-327.

Einum S., Sundt-Hansen L. & Nislow K.H. (2006) The partitioning of density-dependent dispersal, growth and survival throughout ontogeny in a highly fecund organism, *Oikos*, *113*, 489–496.

Einum S. & Kvingedal E. (2011) Relative importance of size-based competitive ability and degree of niche overlap in inter-cohort competition of Atlantic salmon (*Salmo salar*) juveniles, *Canadian Journal of Fisheries and Aquatic Sciences*, *68*(6), 969-976.

Ejarque E., Freixa A., Vazquez E., Guarch A., Amalfitano S., Fazi S., Romaní A.M. & Butturini A. (2017) Quality and reactivity of dissolved organic matter in a Mediterranean river across hydrological and spatial gradients, *Science of The Total Environment*, *599*, 1802-1812.

Elliott J.M. (1972) Rates of gastric evacuation in brown trout, *Salmo trutta L.*, *Freshwater Biology*, *2*(1), 1-18.

Elliott J.M. (1973) The food of brown and rainbow trout (*Salmo trutta* and *S. gairdneri*) in relation to the abundance of drifting invertebrates in a mountain stream, *Oecologia*, *12*, 329-347.

Elliott J.M. (1994) *Quantitative ecology and the brown trout*, Oxford: Oxford University Press.

Elliott J.M., Hurley M.A. & Elliott J.A. (1997) Variable effects of droughts on the density of a sea-trout *Salmo trutta* population over 30 years, *Journal of Applied Ecology*, *34*, 1229-1238.

Elliott J.M. (2000) Pools as refugia for brown trout during two summer droughts: trout responses to thermal and oxygen stress, *Journal of Fish Biology*, *56*(4), 938-948.

Enders E.C., Roy M.L., Ovidio M., Hallot É.J., Boyer C., Petit F. & Roy A.G. (2009) Habitat choice by Atlantic salmon parr in relation to turbulence at a reach scale, *North American Journal of Fisheries Management*, *29*(6), 1819-1830.

Environment Agency (2004) *The State of England's Chalk Rivers*, A Report by the UK Biodiversity Action Plan Steering Group for Chalk Rivers, Bristol, UK.

Environment Agency (2015) South East River Basin Management Plan: Part 1, Bristol.

Environment Agency (2019) *Test and Itchen Abstraction Licencing Strategy*, A strategy to manage water resources sustainably, Version 3, Bristol, UK.

Evans D. (2017) The threat of drier summers to agriculture and the environment in eastern England, *Proceedings of the Institution of Civil Engineers-Engineering Sustainability*, *170*(4), 207-213.

Extence C.A., Balbi D.M. & Chadd R.P. (1999) River flow indexing using british benthic macroinvertebrates: a framework for setting hydroecological objectives, *Regulated Rivers: Research & Management*, *574*, 543-574.

Extence C.A, Chadd R.P, England J., Dunbar M.J, Wood P.J. & Taylor E.D (2013) The assessment of fine sediment accumulation in rivers using macro-invertebrate community response, *River Research and Applications*, *29*(1), 17-55.

Fabris L., Buddendorf W.B. & Soulsby C. (2019) Assessing the seasonal effect of flow regimes on availability of Atlantic salmon fry habitat in an upland Scottish stream, *Science of The Total Environment*, *696*.

Fausch K.D. (1984) Profitable stream positions for salmonids: relating specific growth rate to net energy gain, *Canadian Journal of Zoology*, *62*, 441-451.

Feld C.K., De Bello F. & Dolédec, S. (2014) Biodiversity of traits and species both show weak responses to hydromorphological alteration in lowland river macroinvertebrates, *Freshwater Biology*, *59*(2), 233-248.

Fernandes W.P.A., Griffiths S.W., Ibbotson A.T., Bruford M.W. & Riley W.D. (2015) The role of density and relatedness in wild juvenile Atlantic salmon growth, *Journal of Zoology*, *295*(1), 56-64.

Floury M., Colombet J. & Desvilettes C. (2018) Interspecific competition between restocked 0+ salmon parr (*Salmo salar*) and native fish species in a large European river*, Ecology of Freshwater Fish, 28*(1), 69-84.

Fochetti R., Amici I. & Argano R. (2003) Seasonal changes and selectivity in the diet of brown trout in the River Nera (Central Italy), *Journal of Freshwater Ecology*, *18*(3), 437-444.

Folegot S., Hannah D.M., Dugdale S.J., Kurz M.J., Drummond J.D., Klaar M.J., Lee-Cullin J., Keller T., Martí E., Zarnetske J.P. & Ward A.S. (2018) Low flow controls on stream thermal dynamics, *Limnologica*, *68*, 157-167.

Fornaroli R., Cabrini R., Sartori L., Marazzi F., Canobbio S. & Mezzanotte V. (2016) Optimal flow for brown trout: Habitat – prey optimization, *Science of The Total Environment*, 566, 1568-1578.

Franklin P., Dunbar M. & Whitehead P. (2008) Flow controls on lowland river macrophytes: a review, *Science of the Total Environment*, *400*(1-3), 369-378.

Fraser N.H., Metcalfe N.B., Heggenes J. & Thorpe J.E. (1995) Low summer temperatures cause juvenile Atlantic salmon to become nocturnal, *Canadian Journal of Zoology*, *73*(3), 446-451.

Freeman M.C., Bowen Z.H., Bovee K.D. & Irwin E.R. (2001) Flow and habitat effects on juvenile fish abundance in natural and altered flow regimes, *Ecological Applications*, *11*, 179-190.

French W.E., Vondracek B., Ferrington L.C., Finlay J.C. & Dieterman D.J. (2016) Winter diet of brown trout Salmo trutta in groundwater-dominated streams: influence of environmental factors on spatial and temporal variation, *Journal of Fish Biology*, *89*(5), 2449-2464.

Froese R. (2006) Cube law, condition factor and weight–length relationships: history, meta-analysis and recommendations, *Journal of Applied Ichthyology*, 22(4), 241-253.

Galib S.M. (2020) *The ecological impacts of signal crayfish in upland stream ecosystems,* Doctoral dissertation, Durham University.

Gallagher S.P., Ferreira J., Lang E., Holloway W. & Wright D.W. (2014) Investigation of the relationship between physical habitat and salmonid abundance in two coastal northern California streams, *California Fish and Game*, *100*(4), 683-702.

Ganihar S.R. (1997) Biomass estimates of terrestrial arthropods based on body length, *Journal of Biosciences, 22*, 219-224.

Gibson C.A., Meyer J.L., Poff N.L., Hay L.E. & Georgakakos A. (2005) Flow regime alterations under changing climate in two river basins: implications for freshwater ecosystems, *River Research and Applications*, *21*(8), 849-864.

Giles D.M., Lowings V.A. & Midgley P. (1988) River regulation by seasonal groundwater abstraction: The case of the River Itchen, *Regulated Rivers: Research & Management, 2*(3), 335-347.

Giller P. & Greenberg L. (2015) The relationship between individual habitat use and diet in brown trout, *Freshwater Biology*, *60*(2), 256-266.

Gillson J.P., Maxwell D.M., Gregory S.D., Posen P.E., Riley W.D., Picken J. & Assunção M.G.L. (in review) Identifying important aspects of the flow regime associated with densities of juvenile (age-0+) Atlantic salmon (*Salmo salar*) and trout (*Salmo trutta*) using long-term data from UK rivers, *Freshwater Biology*.

Gippel C.J. & Stewardson M.J. (1998) Use of wetted perimeter in defining minimum environmental flows, *Regulated Rivers: Research & Management*, *14*(1), 53-67.

Girard I.L., Grant J.W. & Steingrímsson S.Ó. (2004) Foraging, growth, and loss rate of young-of-the-year Atlantic salmon (*Salmo salar*) in relation to habitat use in Catamaran Brook, New Brunswick, *Canadian Journal of Fisheries and Aquatic Sciences*, *61*(12), 2339-2349.

González J.M., Recuerda M. & Elosegi A. (2018) Crowded waters: short-term response of invertebrate drift to water abstraction, *Hydrobiologia*, *819*, 39-51.

Gordon N.D., McMahon T.A., Finlayson B.L. & Gippel C.J. (2004) *Stream hydrology: an introduction for ecologists*, 2nd edition, John Wiley and Sons, West Sussex, UK.

Gore J.A., Layzer J.B. & Mead J. (2001) Macroinvertebrate instream flow studies after 20 years: a role in stream management and restoration, *Regulated Rivers: Research & Management*, *17*(45), 527-542.

Gowan C. & Fausch K.D. (2002) Why do foraging stream salmonids move during summer?, *Environmental Biology of Fishes*, *64*(1-3), 139-153.

Graham C.T. & Harrod C. (2009) Implications of climate change for the fishes of the British Isles, *Journal of Fish Biology*, *74*(6), 1143-1205.

Grant J.W., Weir L.K. & Steingrímsson S.Ó. (2017) Territory size decreases minimally with increasing food abundance in stream salmonids: Implications for population regulation, *Journal of Animal Ecology*, *86*(6), 1308-1316**.**

Green J.C. (2006) Effect of macrophyte spatial variability on channel resistance, *Advances in Water Resources*, *29*, 426–438.

Greenberg L.A. (1994) Effects of predation, trout density and discharge on habitat use by brown trout, *Salmo trutta*, in artificial streams, *Freshwater Biology*, *32*(1), 1-11.

Greenberg L.A. & Giller P.S. (2001) Individual variation in habitat use and growth of male and female brown trout, *Ecography*, *24*, 212-224.

Gregory S.D., Armstrong J.D. & Britton J.R. (2018) Is bigger really better? Towards improved models for testing how Atlantic salmon *Salmo salar* smolt size affects marine survival, *Journal of Fish Biology*, *92*(3), 579-592.

Gries G., Whalen K.G., Juanes F. & Parrish D.L. (1997) Nocturnal activity of juvenile Atlantic salmon (*Salmo salar*) in late summer: evidence of diel activity partitioning, *Canadian Journal of Fisheries and Aquatic Sciences*, *54*(6), 1408-1413.

Gries G. & Juanes F. (1998) Microhabitat use by juvenile Atlantic salmon (*Salmo salar*) sheltering during the day in summer, *Canadian Journal of Zoology*, *76*(8), 1441-1449.

Grossman G.D., Carline R.F. & Wagner T. (2017) Population dynamics of brown trout (*Salmo trutta*) in Spruce Creek Pennsylvania: A quarter-century perspective, *Freshwater Biology*, *62*(7), 1143-1154.

Growns I., Murphy J.F. & Jones J.I. (2017) The effects of altered flow and bed sediment on macroinvertebrates in stream mesocosms, *Marine and Freshwater Research*, *68*(3), 496-505.

Gunnarsson G.S. & Steingrímsson S.Ó. (2011) Contrasting patterns of territoriality and foraging mode in two stream-dwelling salmonids, Arctic char (*Salvelinus alpinus*) and brown trout (*Salmo trutta*), *Canadian Journal of Fisheries and Aquatic Sciences*, *68*(12), 2090-2100.

Hakala J.P. & Hartman K.J. (2004) Drought effect on stream morphology and brook trout (*Salvelinus fontinalis*) populations in forested headwater streams, *Hydrobiologia*, *515*, 203-213.

Hannah D.M. & Garner G. (2015) River water temperature in the United Kingdom: changes over the 20th century and possible changes over the 21st century, *Progress in Physical Geography*, *39*(1), 68-92.

Harris C.M., Calladine J.R., Wernham C.V. & Park K.J. (2008) Impacts of piscivorous birds on salmonid populations and game fisheries in Scotland: a review, *Wildlife Biology*, *14*(4), 395-412.

Harris R.M., Armitage P.D., Milner A.M. & Ledger M.E. (2007) Replicability of physicochemistry and macroinvertebrate assemblages in stream mesocosms: implications for experimental research, *Freshwater Biology*, *52*(12), 2434-2443.

Harvey B.C., Nakamoto R.J. & White J.L. (2006) Reduced streamflow lowers dry-season growth of rainbow trout in a small stream, *Transactions of the American Fisheries Society*, *135*(4), 998-1005.

Harvey B.C. & Railsback S.F. (2014) Feeding modes in stream salmonid population models: is drift feeding the whole story?, *Environmental Biology of Fishes*, *97*(5), 615-625.

Hauer C., Unfer G., Holzmann H., Schmutz S. & Habersack H. (2013) The impact of discharge change on physical instream habitats and its response to river morphology, *Climatic Change*, *116*(3-4), 827-850.

Hawkins C.P., Hogue J.N., Decker L.M. & Feminella J.W. (1997) Channel morphology, water temperature, and assemblage structure of stream insects, *Journal of the North American Benthological Society*, 16, 728-749.

Hedger R.D., Diserud O.H., Sandlund O.T., Saksgård L., Ugedal O. & Bremset G. (2018) Bias in estimates of electrofishing capture probability of juvenile Atlantic salmon, *Fisheries Research*, *208*, 286-295.

Heggenes J. (1996) Habitat selection by brown trout (*Salmo trutta*) and young Atlantic salmon (*S. salar*) in streams: static and dynamic hydraulic modelling, *Regulated Rivers: Research and Management*, *12*, 155-169.

Heggenes J. & Dokk J.G. (2001) Contrasting temperatures, waterflows, and light: Seasonal habitat selection by young Atlantic salmon and brown trout in a boreonemoral river, *Regulated Rivers Research & Management, 17*, 623-635.

Heggenes J. (2002) Flexible summer habitat selection by wild, allopatric brown trout in lotic environments, *Transactions of the American Fisheries Society*, *131*, 287-298.

Herrera-Pantoja M. & Hiscock K.M. (2008) The effects of climate change on potential groundwater recharge in Great Britain, *Hydrological Processes*, *22*(1), 73-86.

Hesterberg T., Moore D.S., Monaghan S., Clipson A. & Epstein R. (2005) *Bootstrap Methods and Permutation Tests*, In Moore D.S. & McCabe G.P. (eds.), Introduction to the Practice of Statistics, Freeman, New York, U.S.A.

Herzig A. (1974) Some population characteristics of planktonic crustaceans in Neusiedler sea, *Oecologia*, *15*(2), 127-141.

Higley L.G., Pedigo L.P. & Ostlie K.R. (1986) DEGDAY: a program for calculating degree-days, and assumptions behind the degree-day approach, *Environmental Entomology*, *15*, 999–1016.

Hildrew A.G. & Townsend C.R. (1982) Predators and prey in a patchy environment: A freshwater study, *Journal of Animal Ecology*, *51*, 797-815.

HM Government (2011) Natural environment white paper implementation update, UK.

Hoffmann W.A. & Poorter H. (2002) Avoiding bias in calculations of relative growth rate, *Annals of Botany*, *90*(1), 37-42.

Hogan R. (2006) How to combine errors, http://www.met.rdg.ac.uk/~swrhgnrj/combining_errors.pdf.

Höjesjö J., Kaspersson R. & Armstrong J.D. (2015) Size-related habitat use in juvenile Atlantic salmon: the importance of intercohort competition, *Canadian Journal of Fisheries and Aquatic Sciences*, *73*(8), 1182-1189.

Honkanen H.M., Boylan P., Dodd J.A. & Adams C.E. (2019) Life stage-specific, stochastic environmental effects overlay density dependence in an Atlantic salmon population, *Ecology of Freshwater Fish*, *28*(1), 156-166.

Hook M. & Tang X. (2013) Depletion of fossil fuels and anthropogenic climate change—A review, *Energy Policy*, *52*, 797-809.

Hopkins K.D. (1992) Reporting fish growth: A review of the basics 1, *Journal of the World Aquaculture Society*, *23*(3), 173-179.

Hostetter N.J., Evans A.F., Roby D.D. & Collis K. (2012) Susceptibility of juvenile steelhead to avian predation: the influence of individual fish characteristics and river conditions, *Transactions of the American Fisheries Society*, *141*(6), 1586-1599.

House A.R., Thompson J.R., Roberts C., Smeth K., Old G. & Acreman M.C. (2017) Projecting impacts of climate change on habitat availability in a macrophyte dominated Chalk River, *Ecohydrology*, *10*(4), 1-13.

Hrachowitz M., Soulsby C., Imholt C., Malcolm I.A. & Tetzlaff D. (2010) Thermal regimes in a large upland salmon river: a simple model to identify the influence of landscape controls and climate change on maximum temperatures, *Hydrological Processes*, *24*(23), 3374-3391.

Hubert W.A., Harris D.D. & Wesche T.A. (1994) Diurnal shifts in use of summer habitat by age-0 brown trout in a regulated mountain stream, *Hydrobiologia*, *284*(2), 147-156.

Hughes N.F. & Dill L.M. (1990) Position choice by drift feeding salmonids: model and test for Arctic grayling (*Thymallus arcticus*) in subarctic mountain streams, interior Alaska, *Canadian Journal of Fisheries and Aquatic Sciences*, *47*, 2039-2048.

Hughes N.F. (1992) Selection of positions by drift-feeding salmonids in dominance hierarchies? model and test for Arctic grayling (*thynallus arcticus*) in sub-arctic mountain streams, interior Alaska, *Canadian Journal of Fisheries and Aquatic Science*, *49*, 1999-2008.

Hyvärinen P. & Huusko A. (2006) Diet of brown trout in relation to variation in abundance and size of pelagic fish prey, *Journal of Fish Biology*, *68*(1), 87-98.

Ikediashi C., Paris J.R., King R.A., Beaumont W.R.C., Ibbotson A. & Stevens J.R. (2018) Atlantic salmon *Salmo salar* in the chalk streams of England are genetically unique, *Journal of Fish Biology*, *92*(3), 621-641.

Imre I. & Boisclair D. (2004) Age effects on diel activity patterns of juvenile Atlantic salmon: parr are more nocturnal than young-of-the-year, *Journal of Fish Biology*, *64*(6), 1731-1736.

Ivlev V.S. (1961) *Experimental ecology of the feeding of fishes*, University Microfilms.

Jackson C.R., Meister R. & Prudhomme C. (2011) Modelling the effects of climate change and its uncertainty on UK Chalk groundwater resources from an ensemble of global climate model projections, *Journal of Hydrology*, *399*(1-2), 12-28.

James A.B.W., Dewson Z.S. & Death R.G. (2008a) Do stream macroinvertebrates use instream refugia in response to severe short-term flow reduction in New Zealand streams?, *Freshwater Biology*, *53*(7), 1316-1334.

James A.B.W., Dewson Z.S. & Death R.G. (2008b) The effect of experimental flow reductions on macroinvertebrate drift in natural and streamside channels, *River research and Applications*, *24*(1), 22-35.

Jenkins R.A., Wade K.R. & Pugh E. (1984) Macroinvertebrate–habitat relationships in the River Teifi catchment and the significance to conservation, *Freshwater Biology*, *14*(1), 23-42.

Jensen H., Bøhn T., Amundsen P.A. & Aspholm P.E (2004) Feeding ecology of piscivorous brown trout (*Salmo trutta* L.) in a subarctic watercourse, *Annales Zoologici Fennici*, *41*, 319–328.

Johnson A.C., Acreman M.C., Dunbar M.J., Feist S.W., Giacomello A.M., Gozlan R.E., Hinsley S.A., Ibbotson A.T., Jarvie H.P., Jones J.I. & Longshaw M. (2009) The British river of the future: how climate change and human activity might affect two contrasting river ecosystems in England, *Science of the Total Environment*, *407*(17), 4787-4798.

Johnson J.H. & McKenna J.E. (2015) Diel Resource Partitioning among Juvenile Atlantic Salmon, Brown Trout, and Rainbow Trout during Summer, *North American Journal of Fisheries Management*, *35*(3), 586-597.

Johnson J.H., Dirado J.A., Mackey G. & Abbett R. (2017) Comparative diets and foraging strategies of subyearling Atlantic salmon, brown trout, and rainbow trout during winter, *Journal of Applied Ichthyology*, *33*(6), 1158-1165.

Jones J.I., Moss B., Eaton J.W. & Young J.O. (2000) Do submerged aquatic plants influence periphyton community composition for the benefit of invertebrate mutualists?, *Freshwater Biology*, *43*(4), 591-604.

Jones J.I., Collins A.L., Naden P.S. & Sear D.A. (2012) The relationship between fine sediment and macrophytes in rivers, *River Research and Applications*, *28*(7), 1006-1018.

Jones J.I., Duerdoth C.P., Collins A.L., Naden P.S. & Sear D.S. (2014) Interactions between diatoms and fine sediment, *Hydrological Processes, 28*, 1226-1237.

Jones J.I., Growns I., Arnold A., McCall S. & Bowes M. (2015) The effects of increased flow and fine sediment on hyporheic invertebrates and nutrients in stream mesocosms, *Freshwater Biology*, *60*(4), 813-826.

Jones N.E. & Petreman I.C. (2013) Relating extremes of flow and air temperature to stream fish communities, *Ecohydrology*, *6*(5),826-835.

Jonsson N. & Jonsson B. (1998) Body composition and energy allocation in life-history stages of brown trout, *Journal of Fish Biology*, *53*(6), 1306-1316.

Jonsson B. & Jonsson N. (2009) A review of the likely effects of climate change on anadromous Atlantic salmon *Salmo salar* and brown trout *Salmo trutta*, with particular reference to water temperature and flow, *Journal of Fish Biology*, *75*(10), 2381-2447.

Jowett I.G., Richardson J. & Bonnett M.L. (2005) Relationship between flow regime and fish abundances in a gravel-bed river, New Zealand, *Journal of Fish Biology*, *66*, 1-18

Kahilainen K. & Lehtonen H. (2002) Brown trout (*Salmo trutta* L.) and Arctic charr (*Salvelinus alpinus* (L.)) as predators on three sympatric whitefish (*Coregonus lavaretus* (L.)) forms in the subarctic Lake Muddusjärvi, *Ecology of Freshwater Fish*, *11*, 158-167.

Kahler T.H., Roni P. & Quinn T.P. (2001) Summer movement and growth of juvenile anadromous salmonids in small western Washington streams, *Canadian Journal of Fisheries and Aquatic Sciences*, *58*(10), 1947-1956.

Kakouei K., Kiesel J., Domisch S., Irving K.S., Jähnig S.C. & Kail J. (2018) Projected effects of Climate-change-induced flow alterations on stream macroinvertebrate abundances, *Ecology and Evolution*, *8*(6), 3393-3409.

Kalleberg H. (1958) Observations in a stream tank of territoriality and competition in juvenile salmon and trout (*Salmo salar L*. and *S. trutta L.*), *Report Institute of Freshwater Research*, *39*, 55-98.

Kaspersson R. & Höjesjö J. (2009) Density-dependent growth rate in an age-structured population: a field study on stream-dwelling brown trout *Salmo trutta*, *Journal of Fish Biology*, *74*, 2196-2215.

Kaylor M.J., White S.M., Saunders W.C. & Warren D.R. (2019) Relating spatial patterns of stream metabolism to distributions of juveniles salmonids at the river network scale, *Ecosphere*, *10*(6).

Keeley E.R. & Grant J.W. (1995) Allometric and environmental correlates of territory size in juvenile Atlantic salmon (*Salmo salar*), *Canadian Journal of Fisheries and Aquatic Sciences*, *52*(1), 186-196.

Keeley E.R. & Grant J.W. (1997) Allometry of diet selectivity in juvenile Atlantic salmon (*Salmo salar), Canadian Journal of Fisheries and Aquatic Sciences*, *54*(8), 1894-1902.

Keeley E.R. (2000) An experimental analysis of territory size in juvenile steelhead trout, *Animal Behaviour*, *59*(3), 477-490.

Keeley E.R. & Grant J.W. (2001) Prey size of salmonid fishes in streams, lakes, and oceans, *Canadian Journal of Fisheries and Aquatic Sciences*, *58*(6), 1122-1132.

Kemp P.S., Gilvear D.J. & Armstrong J.D. (2003) Do juvenile Atlantic salmon parr track local changes in water velocity?, *River Research and Applications*, *19*(5-6), 569-575.

Kemp P., Sear D., Collins A., Naden P. & Jones I. (2011) The impacts of fine sediment on riverine fish, *Hydrological Processes*, *25*(11), 1800-1821.

Kennedy G.J.A. & Strange C.D. (1982) The distribution of salmonids in upland streams in relation to depth and gradient, *Journal of Fish Biology*, *20*, 579-591.

Kennedy G.J.A. & Greer J.E. (1988) Predation by cormorants *Phalacrocorax carbo* (L.), on the salmonid populations of an Irish river, *Aquaculture and Fisheries Management*, *19*, 159-170.

Kim J.W., Wood J.L., Grant J.W. & Brown G.E. (2011) Acute and chronic increases in predation risk affect the territorial behaviour of juvenile Atlantic salmon in the wild, *Animal Behaviour*, *81*(1), 93-99.

Kleeberg A., Köhler J.A.N., Sukhodolova T. & Sukhodolov A. (2010) Effects of aquatic macrophytes on organic matter deposition, resuspension and phosphorus entrainment in a lowland river, *Freshwater Biology*, *55*(2), 326-345.

Koljonen S., Huusko A., Mäki-Petäys A., Louhi P. & Muotka T. (2013) Assessing habitat suitability for juvenile Atlantic salmon in relation to in-stream restoration and discharge variability, *Restoration Ecology*, *21*(3), 344-352.

Kominoski J.S. & Pringle C.M. (2009) Resource–consumer diversity: testing the effects of leaf litter species diversity on stream macroinvertebrate communities, *Freshwater Biology*, *54*(7), 1461-1473.

Kraft M.E. (1972) Effects of controlled flow reduction on a trout stream, *Journal of the Fisheries Research Board of Canada*, *29*, 1405-1411.

Krzywinski M. & Altman N. (2013) Points of significance: Power and sample size, *Nature Methods*, *10*, 1139 -1140

Lake P.S. (2003) Ecological effects of perturbation by drought in owing waters, *Freshwater Biology*, *48*, 1161-1172.

Lake P.S. (2011) *Drought and Aquatic Ecosystems: Effects and Responses*, John Wiley and Sons, Chichester, UK.

Lamberti G.A. & Resh V.H. (1983) Stream periphyton and insect herbivores: an experimental study of grazing by a caddisfly population, *Ecology*, *64*(5), 1124-1135.

Lancaster J. & Ledger M.E. (2015) Population-level responses of stream macroinvertebrates to drying can be density-independent or density-dependent, *Freshwater Biology, 60*(12), 2559–2570.

Lange K., Townsend C.R., Gabrielsson R., Chanut P.C. & Matthaei C.D. (2014) Responses of stream fish populations to farming intensity and water abstraction in an agricultural catchment, *Freshwater Biology*, *59*(2), 286-299.

Larsen S., Pace G. & Ormerod S.J. (2011) Experimental effects of sediment deposition on the structure and function of macroinvertebrate assemblages in temperate streams, *River Research and Applications*, *27*(2), 257-267.

Ledger M.E., Edwards F.K., Brown L.E., Milner A.M. & Woodward G. (2011) Impact of simulated drought on ecosystem biomass production: an experimental test in stream mesocosms, *Global Change Biology*, *17*(7), 2288-2297.

Ledger M.E., Harris R.M.L., Armitage P.D. & Milner A.M. (2012) Climate Change Impacts on Community Resilience: Evidence from a drought disturbance experiment, *Advances in Ecological Research*, *46*, 211-258.

Ledger M.E., Brown L.E., Edwards F.K., Hudson L.N., Milner A.M. & Woodward G. (2013) Extreme climatic events alter aquatic food webs: a synthesis of evidence from a mesocosm drought experiment, *Advances in Ecological Research, 48*, 343-395.

Leung E.S., Rosenfeld J.S. & Bernhardt J.R. (2009) Habitat effects on invertebrate drift in a small trout stream: implications for prey availability to drift-feeding fish, *Hydrobiologia*, *623*(1), 113-125.

Lindeman A.A., Grant J.W. & Desjardins C.M. (2015) Density-dependent territory size and individual growth rate in juvenile Atlantic salmon (*Salmo salar*), *Ecology of Freshwater Fish*, *24*(1), 15-22.

López-Olmeda J.F., Noble C. & Sánchez-Vázquez F.J. (2012) Does feeding time affect fish welfare?, *Fish Physiology and Biochemistry*, *38*(1), 143-152.

Luhar M., Rominger J. & Nepf H. (2008) Interaction between flow, transport and vegetation spatial structure, *Environmental Fluid Mechanics*, *8*, 423–439.

Lytle D.A. & Poff N.L. (2004) Adaptation to natural flow regimes, *Trends in Ecology & Evolution*, *19*(2), 94-100.

Lytle D.A. (2008) *Life-history and behavioural adaptations to flow regime in aquatic insects*, In Lancaster J. & Briers R.A (eds), Aquatic Insects: Challenges to Populations, CAB International, Wallingford, UK: 122-138

Mackey A.P. & Berrie A.D. (1991) The prediction of water temperatures in chalk streams from air temperatures, *Hydrobiologia*, *210*(3), 183-189.

Macnaughton C.J., McLaughlin F., Bourque G., Senay C., Lanthier G., Harvey-Lavoie S., Legendre P., Lapointe M. & Boisclair D. (2015) The Effects of Regional Hydrologic Alteration on Fish Community Structure in Regulated Rivers, *River Research and Applications*, *33*(2), 249-257.

Maddock I. (1999) The importance of physical habitat assessment for evaluating river health, *Freshwater Biology*, *41*(2), 373-391.

Malcolm I.A., Soulsby C., Hannah D.M., Bacon P.J., Youngson A.F. & Tetzlaff D. (2008) The influence of riparian woodland on stream temperatures: implications for the performance of juvenile salmonids, *Hydrological Processes*, *22*(7), 968-979.

Mann R.H.K., Blackburn J.H. & Beaumont W.R.C. (1989) The ecology of brown trout (*Salmo trutta*) in English chalk streams, *Freshwater Biology*, *21*(1), 57-70.

Martel G. (1996) Growth rate and influence of predation risk on territoriality in juvenile coho salmon (*Oncorhynchus kisutch*), *Canadian Journal of Fisheries and Aquatic Sciences*, *53*(3), 660-669.

Marsh T.J. & Hannaford J. (2008) *UK Hydrodynamic Register*, In: Hydrological data UK series, Centre for Ecology & Hydrology, Wallingford.

Mason C.F. (1977) Populations and Production of Benthic Animals in two Contrasting Shallow Lakes in Norfolk, *The Journal of Animal Ecology*, *46*(1), 147-172.

McDevitt-Galles T. & Johnson P.T. (2018) Drought attenuates the impact of fish on aquatic macroinvertebrate richness and community composition, *Freshwater Biology*, *63*(11), 1457-1468.

McGuigan K., Franklin C.E., Moritz C. & Blows M.W. (2003) Adaptation of rainbow fish to lake and stream habitats, *Evolution*, *57*(1), 104-118.

McKenna J.E., Reeves H.W. & Seelbach P.W. (2018) Measuring and evaluating ecological flows from streams to regions: Steps towards national coverage, *Freshwater Biology*, *63*(8), 874-890.

Metcalfe N.B., Valdimarsson S.K. & Fraser N.H.C. (1997) Habitat profitability and choice in a sit-and-wait predator: juvenile salmon prefer slower currents on darker nights, *Journal of Animal Ecology*, *66*, 866 -875.

Metcalfe N.B., Fraser N.H. & Burns M.D. (1998) State–dependent shifts between nocturnal and diurnal activity in salmon, *Proceedings of the Royal Society of London. Series B: Biological Sciences*, *265*(1405), 1503-1507.

Metcalfe N.B., Fraser N.H., & Burns M.D. (1999) Food availability and the nocturnal vs. diurnal foraging trade-off in juvenile salmon, *Journal of Animal Ecology*, *68*(2), 371-81.

Meyer E. (1989) The relationship between body length parameters and dry mass in running water macroinvertebrates, *Fundamental and Applied Limnology*, *117*, 191-203.

Milhous R.T., Updike M.A. & Schneider X. (1989) *Physical Habitat Simulation System Reference Manual – Version 2*, Instream Flow Information Paper 26, U.S. Fish and Wildlife Service Biological Report 89.

Milner A.M., Picken J.L., Klaar M.J., Robertson A.L., Clitherow L.R., Eagle L. & Brown L.E. (2018) River ecosystem resilience to extreme flood events, *Ecology and Evolution*, *8*(16), 8354-8363.

Milner N.J. (1982) Habitat Evaluation in Salmonid Streams, Proceeding of the 13th Annual Study course, West Bridgford: Institute of Fisheries Management, 47-65.

Milner N.J., Elliott J.M., Armstrong J.D., Gardiner R., Welton J.S. & Ladle M. (2003) The natural control of salmon and trout populations in streams, *Fisheries Research*, *62*(2), 111-125.

Minshall G.W. & Winger P.V. (1968) The effect of reduction in stream flow on invertebrate drift, *Ecology*, *49*(3), 580-582.

Mitchell J.F. (1989) The "greenhouse" effect and climate change, *Reviews of Geophysics*, *27*(1), 115-139.

Monk W.A., Wood P.J., Hannah D.M., Wilson D.A., Extence C.A. & Chadd R.P. (2006) Flow variability and macroinvertebrate community response within riverine systems, *River Research and Applications*, *22*(5), 595-615.

Monk W.A., Wood P.J., Hannah D.M., Extence C.A., Chadd R.P. & Dunbar M.J. (2012) How does macroinvertebrate taxonomic resolution influence ecohydrological relationships in riverine ecosystems, *Ecohydrology*, *5*(1), 36-45.

Morrell L.J. & Kokko H. (2003) Adaptive strategies of territory formation, *Behavioral Ecology and Sociobiology*, *54*(4), 385-395.

Murphy J.M., Sexton D.M., Jenkins G.J., Boorman P.M., Booth B.B., Brown C.C., Clark R.T., Collins M., Harris G.R., Kendon E.J. & Betts R.A. (2009) *UK Climate Projections Science Report: climate change projections*, Met Office Hadley Centre, Exeter, UK.

Musseau C., Vincenzi S., Jesenšek D., Cantera I., Boulêtreau S., Santoul F. & Crivelli, A.J. (2015) Direct and indirect effects of environmental factors on dietary niches in size-structured populations of a wild salmonid, *Ecosphere*, *6*(12), 1-15.

Naden P.S., Murphy J.F., Old G.H., Newman J., Scarlett P., Harman M., Duerdoth C.P., Hawczak A., Pretty J.L., Arnold A. & Laizé C. (2016) Understanding the controls on deposited fine sediment in the streams of agricultural catchments, *Science of the Total Environment*, *547*, 366-381.

Naiman R.J. & Latterell J.J. (2005) Principles for linking fish habitat to fisheries management and conservation, *Journal of Fish Biology*, *67*, 166-185.

Nakano S., Fausch K.D. & Kitano S. (1999) Flexible niche partitioning via a foraging mode shift: a proposed mechanism for coexistence in stream-dwelling charr, *Journal of Animal Ecology*, *68*(6), 1079-1092.

Naman S.M., Rosenfeld J.S. & Richardson J.S. (2016) Causes and consequences of invertebrate drift in running waters: from individuals to populations and trophic fluxes, *Canadian Journal of Fisheries and Aquatic Sciences*, *73*(8), 1292-1305.

Neale M.W., Dunbar M.J., Jones J.I. & Ibbotson A.T. (2008) A comparison of the relative contributions of temporal and spatial variation in the density of drifting invertebrates in a Dorset (UK) chalk stream, *Freshwater Biology*, *53*(8), 1513-1523.

Neuheimer A.B. & Taggart C.T. (2007) The growing degree-day and fish size-at-age: the overlooked metric, *Canadian Journal of Fisheries and Aquatic Sciences*, *64*(2), 375-385.

Nicola G.G., Ayllón D., Elvira B. & Almodóvar A. (2015) Territorial and foraging behaviour of juvenile Mediterranean trout under changing conditions of food and competitors, *Canadian Journal of Fisheries and Aquatic Sciences*, *73*(6), 990-998.

Niemela E., Julkunen M. & Erkinaro J. (2000) Quantitative electrofishing for juvenile salmon densities: Assessment of the catchability during a long-term monitoring programme, *Fisheries Research*, *48*, 15-22.

Nislow K.H., Folt C. & Seandel M. (1998) Food and foraging behavior in relation to microhabitat use and survival of age-0 Atlantic salmon, *Canadian Journal of Fisheries and Aquatic Sciences*, *55*(1), 116-127.

Nislow K.H. & Armstrong J.D. (2012) Towards a life-history-based management framework for the effects of flow on juvenile salmonids in streams and rivers, *Fisheries Management and Ecology*, *19*(6), 451-463.

NOAA National Centers for Environmental Information (2019a) *State of the Climate: Global Climate Report for Annual 2018*, https://www.ncdc.noaa.gov/sotc/global/201813, accessed 30/06/2019.

NOAA National Centers for Environmental Information (2019b) *State of the Climate: Global Climate Report for May 2019*, https://www.ncdc.noaa.gov/sotc/global/201905, accessed 30/06/2019.

Nordwall F., Näslund I. & Degerman E. (2001) Intercohort competition effects on survival, movement, and growth of brown trout (*Salmo trutta*) in Swedish streams, *Canadian Journal of Fisheries and Aquatic Sciences*, *58*(11), 2298-2308.

Nuhfer A.J., Zorn T.G. & Wills T.C. (2017) Effects of reduced summer flows on the brook trout population and temperatures of a groundwater-influenced stream, *Ecology of Freshwater Fish*, *26*(1), 108-119.

Nunn A.D., Tewson L.H. & Cowx I.G. (2012) The foraging ecology of larval and juvenile fishes, *Reviews in Fish Biology and Fisheries*, *22*(2), 377-408.

Nystrom P.E.R. & Strand J. (1996) Grazing by a native and an exotic crayfish on aquatic macrophytes, *Freshwater Biology*, *36*(3), 673-682.

O'Connor C.M. & Cooke S.J. (2015) Ecological carryover effects complicate conservation, *Ambio*, *44*(6), 582-591.

O'Neill R. & Hughes K. (2014) *The State of England's Chalk Streams,* WWF-UK, Surrey, UK.

Ogle D.H., Wheeler P. & Dinno A. (2018) *FSA: Fisheries Stock Analysis*, R package version 0.8.21.9000, https://github.com/droglenc/FSA.

Ohlberger J., Buehrens T.W., Brenkman S.J., Crain P., Quinn T.P. & Hilborn R. (2018) Effects of past and projected river discharge variability on freshwater production in an anadromous fish, *Freshwater Biology*, *63*(4), 331-340.

Oksanen J., Blanchet F.G., Kindt R., Legendre P., Minchin P.R., O'hara R.B., Simpson G.L., Solymos P., Stevens M.H.H., Wagner H. & Oksanen M.J. (2013) Package 'vegan', *Community ecology package,* version 2.5-3, *2*(9).

Orpwood J.E., Griffiths S.W. & Armstrong J.D. (2006) Effects of food availability on temporal activity patterns and growth of Atlantic salmon, *Journal of Animal Ecology*, *75*, 677–685.

Ovidio M., Baras E., Goffaux D., Giroux F. & Philippart J.C. (2002) Seasonal variations of activity pattern of brown trout (*Salmo trutta*) in a small stream, as determined by radio-telemetry, *Hydrobiologia*, *470*(1-3), 195-202.

Park Y.S., Grenouillet G., Esperance B. & Lek S. (2006) Stream fish assemblages and basin land cover in a river network, *Science of the Total Environment*, *365*, 140-153.

Parry E.S., Gregory S.D., Lauridsen R.B. & Griffiths S.W. (2018) The effects of flow on Atlantic salmon (*Salmo salar*) redd distribution in a UK chalk stream between 1980 and 2015, *Ecology of Freshwater Fish*, *27*(1), 128-137.

Peckarsky B.L (2011) *Methods in stream ecology*, edited by Hauer F.R. & Lamberti G., Academic Press, 561-583.

Perkins D.M., Reiss J., Yvon-Durocher G. & Woodward G. (2010) Global change and food webs in running waters, *Hydrobiologia*, *657*(1), 181–198.

Petersen J.E. & Englund G. (2005) Dimensional approaches to designing better experimental eco-systems: a practitioner's guide with examples, *Oecologia*, *145*, 216-224.

Petts G.E., Nestler J. & Kennedy R.H. (2006) Advancing science for water resources management, *Hydrobiologia, 565*(1), 277-288.

Petty J.T., Hansbarger J.L., Huntsman B.M. & Mazik P.M. (2012) Brook trout movement in response to temperature, flow, and thermal refugia within a complex Appalachian riverscape, *Transactions of the American Fisheries Society*, *141*(4), 1060-1073.

Phang S.C., Stillman R.A., Cucherousset J., Britton J.R., Roberts D., Beaumont W.R.C. & Gozlan R.E. (2016) FishMORPH-An agent-based model to predict salmonid growth and distribution responses under natural and low flows, *Scientific reports*, *6.*

Piccolo J.J., Frank B.M. & Hayes J.W. (2014) Food and space revisited: The role of drift-feeding theory in predicting the distribution, growth, and abundance of stream salmonids, *Environmental Biology of Fishes*, *97*(5), 475-488.

Pimm S.L. (1984) The complexity and stability of ecosystems, *Nature*, *307*, 321–326.

Poff N.L. (1992) Why Disturbances Can Be Predictable: A Perspective on the Definition of Disturbance in Streams, *Journal of the North American Benthological Society, 11*(1), 86–92.

Poff N.L., Allan J.D., Bain M.B., Karr J.R., Prestegaard K.L., Richter B.D., Sparks R.E. & Stromberg J.C. (1997) The natural flow regime, *BioScience*, 769-784.

Poff N.L., Richter B.D., Arthington A.H., Bunn S.E., Naiman R.J., Kendy E., Acreman M., Apse C., Bledsoe B.P., Freeman M.C. & Henriksen J. (2010) The ecological limits of hydrologic alteration (ELOHA): a new framework for developing regional environmental flow standards, *Freshwater Biology*, *55*(1), 147-170.

Poff N.L. & Zimmerman J.K. (2010) Ecological responses to altered flow regimes: a literature review to inform the science and management of environmental flows, *Freshwater Biology*, *55*(1), 194-205.

Poff N.L. (2018) Beyond the natural flow regime? Broadening the hydro-ecological foundation to meet environmental flows challenges in a non-stationary world, *Freshwater Biology*, *63*(8), 1011-1021.

Post J.R. & Parkinson E.A. (2001) Energy allocation strategy in young fish: allometry and survival, *Ecology*, *82*, 1040-1051.

Power M.E., Sun A., Parker G., Dietrich W.E. & Wootton J.T. (1995) Hydraulic food-chain models, *BioScience*, 45, 159-167.

Power M.E., Holomuzki J.R & Lowe R.L. (2013) Food webs in Mediterranean rivers, *Hydrobiologia*, *719*, 119-136.

Prenda J.O., Armitage P.D. & Grayston A.L (1997) Habitat use by the fish assemblages of two chalk streams, *Journal of Fish Biology*, *51*(1), 64-79.

Pyke G.H. (1984) Optimal foraging theory: a critical review, *Annual Review of Ecology, Evolution, and Systematics*, *15*, 523-575.

R Core Team (2018) R: A language and environment for statistical computing, R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/.

Rader R.B., Belish T., Young M.K. & Rothlisberger J. (2007) The scotopic visual sensitivity of four species of trout: a comparative study, *Western North American Naturalist*, *67*(4), 524-537.

Raikow D., Grubbs S. & Cummins K. (1995) Debris dam dynamics and coarse particulate organic matter retention in an Appalachian Mountain stream, *Journal of the North American Benthological Society, 14*(4), 535-546.

Railsback S.F., Harvey B.C., Hayse J.W. & LaGory K.E. (2005) Tests of theory for diel variation in salmonid feeding activity and habitat use, *Ecology*, 86(4), 47-959.

Reaney S.M., Lane S.N., Heathwaite A.L. & Dugdale L.J. (2011) Risk-based modelling of diffuse land use impacts from rural landscapes upon salmonid fry abundance, *Ecological Modelling*, *222*(4), 1016-1029.

Reebs S.G. (2002) Plasticity of diel and circadian activity rhythms in fishes, *Reviews in Fish Biology and Fisheries, 12*(4), 349-371.

Reid A.J., Carlson A.K., Creed I.F., Eliason E.J., Gell P.A., Johnson P.T., Kidd K.A., MacCormack T.J., Olden J.D., Ormerod S.J. & Smol J.P. (2019) Emerging threats and persistent conservation challenges for freshwater biodiversity, *Biological Reviews*, *94*(3), 849-873.

Reznick D., Ghalambor C. & Nunney L. (2002) The evolution of senescence in fish, *Mechanisms of Ageing and Development*, *123*(7), 773-789.

Richter B.D., Mathews R., Harrison D.L. & Wigington R. (2003) Ecologically sustainable water management: managing river flows for ecological integrity, *Ecological Applications*, *13*(1), 206-224.

Ricker W. E. (1979*) Growth rates and models*, in Hoar W.S, Randall D.J. & Brett J.R. (eds.), Fish physiology, volume VIII, Bioenergetics and growth, Academic Press, New York, USA.

Riley W.D., Eagle M.O., Ives M.J., Rycroft P. & Wilkinson A. (2003) A portable passive integrated transponder multi-point decoder system for monitoring habitat use and behaviour of freshwater fish in small streams, *Fisheries Management and Ecology*, *10*, 265-268.

Riley W.D., Ives M.J., Pawson M.G. & Maxwell D.L. (2006) Seasonal variation in habitat use by salmon, *Salmo salar*, trout, *Salmo trutta* and grayling, *Thymallus thymallus*, in a chalk stream, *Fisheries Management and Ecology*, *13*(4), 221-236.

Riley W.D., Maxwell D.L., Pawson M.G. & Ives M.J. (2009a) The effects of low summer flow on wild salmon (*Salmo salar*), trout (*Salmo trutta*) and grayling (*Thymallus thymallus*) in a small stream, *Freshwater Biology*, *54*(12), 2581-2599.

Riley W.D., Pawson M.G., Quayle V. & Ives M.J. (2009b) The effects of stream canopy management on macroinvertebrate communities and juvenile salmonid production in a chalk stream, *Fisheries Management and Ecology*, *16*(2), 100-111.

Riley W.D., Potter E.C.E., Biggs J., Collins A.L., Jarvie H.P., Jones J.I., Kelly-Quinn M., Ormerod S.J., Sear D. A., Wilby R.L., Broadmeadow S., Brown C.D, Chanin P., Copp G.H., Cowx I.G., Grogan A., Hornby D.D., Huggett D., Kelly M.G., Naura M., Newman J.R. & Siriwardena G.M. (2018) Small Water Bodies in Great Britain and Ireland: Ecosystem function, human-generated degradation, and options for restorative action, *Science of the Total Environment* 645, 1598-1616.

Robinson C.V., Webster T.M.U., Cable J., James J. & Consuegra S. (2018) Simultaneous detection of invasive signal crayfish, endangered white-clawed crayfish and the crayfish plague pathogen using environmental DNA, *Biological Conservation*, *222*, 241-252.

Rolls R.J., Leigh C. & Sheldon F. (2012) Mechanistic effects of low-flow hydrology on riverine ecosystems: ecological principles and consequences of alteration, *Freshwater Science*, *31*(4), 1163-1186.

Rolls R.J. & Arthington A.H. (2014) How do low magnitudes of hydrologic alteration impact riverine fish populations and assemblage characteristics?, *Ecological Indicators*, *39*, 179-188.

Rolls R.J. & Bond N. (2017) *Environmental and ecological effects of flow alteration in surface water ecosystems*, in Horne A., Webb J.A., Stewardson M., Richter B. & Acreman M.C. (Eds.), Water for the Environment: Policy, Science, and Integrated Management, Elsevier, Amsterdam, The Netherlands.

Romaní A.M., Amalfitano S., Artigas J., Fazi S., Sabater S., Timoner X., Ylla I. & Zoppini A. (2013) Microbial biofilm structure and organic matter use in mediterranean streams, *Hydrobiologia*, *719*(1), 43-58.

Rosenfeld J.S & Boss S. (2001) Fitness consequences of habitat use for juvenile Cutthroat Trout: Energetic costs and benefits in pools and riffles, *Canadian Journal of Fisheries and Aquatic Sciences*, *58*, 585-593.

Rosenfeld J.S. & Ptolemy R. (2012) Modelling available habitat versus available energy flux: do PHABSIM applications that neglect prey abundance underestimate optimal flows for juvenile salmonids?, *Canadian Journal of Fisheries and Aquatic Sciences*, *69*(12), 1920-1934.

Rosenfeld J.S. (2017) Developing flow–ecology relationships: implications of nonlinear biological responses for water management, *Freshwater Biology*, *62*(8), 1305-1324.

Roussel J. M. & A. Bardonnet (1999) Ontogeny of diel pattern of stream margin habitat use by emerging Brown Trout, *Salmo trutta*, in experimental channels: influence of food and predator preference, *Environmental Biology of Fish*, 56, 253-262.

Rovira A., Alcaraz C. & Trobajo R. (2016) Effects of plant architecture and water velocity on sediment retention by submerged macrophytes, *Freshwater Biology*, *61*(5), 758-768.

Ryan D.K. & Kelly-Quinn M. (2015) Effects of riparian canopy cover on salmonid diet and prey selectivity in low nutrient streams, *Journal of Fish Biology*, *86*(1), 16-31.

Sabo J.L., Bastow J.L. & Power M.E. (2002) Length-mass relationships for adult aquatic and terrestrial invertebrates in a California watershed, *Journal of the North American Benthological Society*, *21*, 336-343.

Sánchez-Hernández J. & Cobo F. (2012) Summer differences in behavioural feeding habits and use of feeding habitat among brown trout (Pisces) age classes in a temperate area, *Italian Journal of Zoology, 79*(3), 468-478.

Sand-Jensen K. (1998) Influence of submerged macrophytes on sediment composition and near-bed flow in lowland streams, *Freshwater Biology*, *39*, 663-679.

Sanders H., Rice S. & Wood P. (2018) Biotic and abiotic drivers of the burrowing behaviour of invasive signal crayfish (*Pacifastacus leniusculus*): mesocosm experiments, *EGUGA*, 1249.

Sanders I.A., Heppell C.M., Cotton J.A., Wharton G., Hildrew A.G., Flowers E.J. & Trimmer M. (2007) Emission of methane from chalk streams has potential implications for agricultural practices, *Freshwater Biology*, *52*(6), 1176-1186.

Seaburg K.G. (1957) A stomach sampler for live fish, *The Progressive Fish-Culturist*, *19*(3), 137-139.

Sear D.A., Armitage P.D. & Dawson F.H. (1999) Groundwater dominated rivers, *Hydrological Processes*, *13*(3), 255-276.

Slaney P.A. & Northcot T.G. (1974) Effects of prey abundance on density and territorial behaviour of young rainbow trout (*Salmo gairdneri*) in a laboratory stream channel, *Journal of the Fisheries Research Board of Canada*, *31*, 1201-1209.

Slavík O., Horký P., Maciak M., Horká P. & Langrová I. (2018) Diel movement of brown trout, *Salmo trutta*, is reduced in dense populations with high site fidelity, *Ecology and Evolution*, *8*(9), 4495-4507.

Sloman K.A. & Armstrong J.D. (2002) Physiological effects of dominance hierarchies: laboratory artefacts or natural phenomena?, *Journal of Fish Biology*, *61*(1), 1-23.

Smith C. & Reay P. (1991) Cannibalism in teleost fish, *Reviews in Fish Biology and Fisheries*, *1*(1), 41-64.

Smock L.A. (1980) Relationship between body size and biomass of aquatic insects, *Freshwater Biology*, *10*, 375-383.

Sotiropoulos J.C., Nislow K.H. & Ross M.R. (2006) Brook trout, *Salvelinus fontinalis*, microhabitat selection and diet under low summer stream flows, *Fisheries Management and Ecology*, *13*(3), 149-155.

Southern Water (2014) *The River Itchen challenge*, https://www.southernwater.co.uk/itchenchallenge, accessed 19/04/2018.

Speirs D.C., Gurney W.S.C., Hildrew A.G. & Winterbottom J.H. (2000) Long-term demographic balance in the Broadstone stream insect community, *Journal of Animal Ecology*, *69*(1), 45-58.

Spoljar M., Zhang C., Dražina T., Zhao G., Lajtner J. & Radonić G. (2017) Development of submerged macrophyte and epiphyton in a flow-through system: Assessment and modelling predictions in interconnected reservoirs, *Ecological Indicators*, *75*, 145-154.

Steingrímsson S.Ó. & Gíslason G.M. (2002) Body size, diet and growth of landlocked brown trout, *Salmo trutta*, in the subarctic River Laxá, North-East Iceland, *Environmental Biology of Fishes*, *63*(4), 417-426.

Steinman A.D., Lamberti G.A., Leavitt P.R. & Uzarski D.G. (2017) Biomass and pigments of benthic algae, In *Methods in Stream Ecology, Volume 1 (Third Edition)*, 223-241.

Steinmetz J., Kohler S.L. & Soluk D.A. (2003) Birds are overlooked top predators in aquatic food webs, *Ecology*, *84*(5), 1324-1328.

Stewart R.I.A., Bohan D.A., Jeppesen E., Korda R.L., Ledger M.E., Meerhoff M., Moss B., Mulder C., Shurin J.B., Suttle B., Thompson R. & Trimmer M. (2013) Mesocosm experiments as a tool for ecological climate change research, *Advances in Ecological Research*, *48*, 71-181.

Stradmeyer L., Höjesjö J., Griffiths S.W., Gilvear D.J. & Armstrong J.D. (2008) Competition between brown trout and Atlantic salmon parr over pool refuges during rapid dewatering, *Journal of Fish Biology*, *72*(4), 848-860.

Stubbington R., Greenwood A.M., Wood P.J., Armitage P.D., Gunn J. & Robertson A.L. (2009) The response of perennial and temporary headwater stream invertebrate communities to hydrological extremes, *Hydrobiologia*, *630*(1), 299-312.

Suren A.M., Biggs B.J.F., Duncan M.J. & Bergey L. (2003) Benthic community dynamics during summer low-flows in two rivers of contrasting enrichment 2. Invertebrates, *New Zealand Journal of Marine and Freshwater Research*, *37*(1), 71-83.

Sutton S.G., Bult T.P. & Haedrich R.L. (2000) Relationships among fat weight, body weight, water weight, and condition factors in wild Atlantic salmon parr, *Transactions of the American Fisheries Society*, *129*(2), 527-538.

Syrjänen J., Korsu K., Louhi P., Paavola R. & Muotka T. (2011) Stream salmonids as opportunistic foragers: the importance of terrestrial invertebrates along a stream-size gradient, *Canadian Journal of Fisheries and Aquatic Sciences, 68*(12), 2146-2156.

Taulbee W.K., Nietch C.T., Brown D., Ramakrishnan B. & Tompkins M.J. (2009) Ecosystem consequences of contrasting flow regimes in an urban effect stream mesocosm study, *Journal of American Water Resources Association*, *45*, 907-927.

Teichert M.A.K., Kvingedal E., Forseth T., Ugedal O. & Finstad A.G. (2010) Effects of discharge and local density on the growth of juvenile Atlantic salmon *Salmo salar*, *Journal of Fish Biology*, *76*(7), 1751-1769.

Tharme R.E. (2003) A global perspective on environmental flow assessment: emerging trends in the development and application of environmental flow methodologies for rivers, *River Research and Applications*, *19*(5-6), 397-441.

Tonkin J.D., Poff N.L., Bond N.R., Horne A., Merritt D.M., Reynolds L.V., Olden J.D., Ruhi A. & Lytle D.A. (2019) Prepare river ecosystems for an uncertain future, *Nature*, *570*, 301.

Twomey H. & Giller P.S. (1990) Stomach flushing and individual Panjet tattooing of salmonids: an evaluation of the long-term effects on two wild populations, *Aquaculture Research*, *21*(1), 137-142.

Ueding M. (2012) How to combine the error of two independent measurements of the same quantity?, https://physics.stackexchange.com/q/23643.

Vadher A.N., Stubbington R. & Wood P.J. (2015) Fine sediment reduces vertical migrations of Gammarus pulex (Crustacea: Amphipoda) in response to surface water loss, *Hydrobiologia*, *753*(1), 61-71.

Vadher A.N., Leigh C., Millett J., Stubbington R. & Wood P.J. (2017) Vertical movements through subsurface stream sediments by benthic macroinvertebrates during experimental drying are influenced by sediment characteristics and species traits, *Freshwater Biology*, *62*, 1730-1740.

Van Loon A.F., Stahl K., Di Baldassarre G., Clark J., Rangecroft S., Wanders N., Gleeson T., Van Dijk A.I., Tallaksen L.M., Hannaford J. & Uijlenhoet R. (2016) Drought in a human-modified world: reframing drought definitions, understanding, and analysis approaches, *Hydrology and Earth System Sciences*, *20*(9), 3631-3650.

VerWey B.J., Kaylor M.J., Garcia T.S. & Warren D.R. (2018) Effects of a severe drought on summer abundance, growth, and movement of cutthroat trout in a western Oregon headwater stream, *Northwestern Naturalist*, *99*(3), 209-222.

Villeneuve A., Montuelle B. & Bouchez A. (2011) Effects of flow regimes and pesticides on periphyton communities: evolution and role of biodiversity, *Aquatic Toxicology*, *102*, 123-133.

Visser A., Beevers L. & Patidar S. (2019) The Impact of Climate Change on Hydroecological Response in Chalk Streams, *Water, 11*(3), 596.

Vowles A.S. & Kemp P.S. (2019) The importance of seasonal macrophyte cover for the behaviour and performance of brown trout (*Salmo trutta*) in a groundwater-fed river, *Freshwater Biology*.

Walker P.D., Wijnhoven S. & Van Der Velde G. (2013) Macrophyte presence and growth form influence macroinvertebrate community structure, *Aquatic Botany*, *104*, 80-87.

Wall E., Wreford A., Topp K. & Moran D. (2010) Biological and economic consequences heat stress due to a changing climate on UK livestock, *Advances in Animal Biosciences*, *1*(01), 53.

Walters T.F. (1965) Interpretation of invertebrate drift in streams, *Ecology*, *46*(3), 327-334.

Walters A.W. & Post D.M. (2008) An experimental disturbance alters fish size structure but not food chain length in streams, *Ecology*, *89*(12), 3261-3267.

Walters A.W. & Post D.M. (2011) How low can you go? Impacts of a low flow disturbance on aquatic insect communities, *Ecological Applications*, *21*(1), 163-174.

Walters A.W. (2016) The importance of context dependence for under- standing the effects of low-flow events on fish, *Freshwater Science*, *35*, 216-228.

Wang Y., Naumann U., Wright S.T. & Warton D.I. (2012) mvabund- an R package for model-based analysis of multivariate abundance data, *Methods in Ecology and Evolution*, *3*, 471-474.

Ward D.M., Nislow K.H. & Folt C.L. (2009) Increased population density and suppressed prey biomass: relative impacts on juvenile Atlantic salmon growth, *Transactions of the American Fisheries Society*, *138*(1),135-143.

Warfe D.M., Hardie S.A., Uytendaal A.R., Bobbi C.J. & Barmuta L.A. (2014) The ecology of rivers with contrasting flow regimes: identifying indicators for setting environmental flows, *Freshwater Biology*, *59*(10), 2064-2080.

Warren M., Dunbar M.J. & Smith C. (2015) River flow as a determinant of salmonid distribution and abundance: a review, *Environmental Biology of Fishes*, *98*(6), 1695-1717.

Watkins M.S., Doherty S. & Copp G.H. (1997) Microhabitat use by 0+ and older fishes in a small English chalk stream, *Journal of Fish Biology*, *50*(5), 1010-1024.

Webb B.W. & Zhang Y. (1999) Water temperatures and heat budgets in Dorset chalk water courses, *Hydrological Processes*, *13*(3), 309-321.

Weber N., Bouwes N. & Jordan C.E. (2014) Estimation of salmonid habitat growth potential through measurements of invertebrate food abundance and temperature, *Canadian Journal of Fisheries and Aquatic Sciences*, *71*(8), 1158-1170.

Wenn C.L. (2008) Do freshwater macroinvertebrates reflect water quality improvements following the removal of point source pollution from Spen Beck, West Yorkshire?, *Earth & Environment*, *3*, 369-406.

Westwood C.G., England J., Dunbar M.J., Holmes N.T., Leeming D.J. & Hammond D. (2017) An approach to setting ecological flow thresholds for southern English chalk streams, *Water and Environment Journal*, *31*(4), 528-536.

Wheeler K., Wenger S.J. & Freeman M.C. (2018) States and rates: Complementary approaches to developing flow-ecology relationships, *Freshwater Biology*, *63*(8), 906-916.

White J.C., Hannah D.M., House A., Beatson S.J., Martin A. & Wood P.J. (2017) Macroinvertebrate responses to flow and stream temperature variability across regulated and non-regulated rivers, *Ecohydrology*, *10*(1), 1773.

White J.C., House A., Punchard N., Hannah D.M., Wilding N.A. & Wood P.J. (2018) Macroinvertebrate community responses to hydrological controls and groundwater abstraction effects across intermittent and perennial headwater streams, *Science of the Total Environment*, *610*, 1514-1526.

White R.S., McHugh P.A. & McIntosh A.R. (2016) Drought survival is a threshold function of habitat size and population density in a fish metapopulation, *Global Change Biology*, *22*(10), 3341-3348.

White S.L. & Gowan C. (2014) Social learning enhances search image acquisition in foraging brook trout, *Environmental Biology of Fishes*, *97*(5), 523-528.

Wilding N.A., White J.C., Chadd R.P., House A. & Wood P.J. (2018) The influence of flow permanence and drying pattern on macroinvertebrate biomonitoring tools used in the assessment of riverine ecosystems, *Ecological indicators*, *85*, 548-555.

Wills T.C., Baker E.A., Nuhfer A.J. & Zorn T.G. (2006) Response of the benthic macroinvertebrate community in a northern Michigan stream to reduced summer stream flows, *River Research and Applications*, *22*(7), 819-836.

Winfield I.J. (2016) Recreational fisheries in the UK: natural capital, ecosystem services, threats, and management, *Fisheries Science*, *82*(2), 203-212.

Wipfli M.S., Richardson J.S. & Naiman R.J. (2007) Ecological Linkages Between Headwaters and Downstream Ecosystems: Transport of Organic Matter, Invertebrates, and Wood Down Headwater Channels, *Journal of the American Water Resources Association*, *43*(1), 72-85.

Wolnicki J., Myszkowski L., Korwin-kossakowski M., Kamiński R. & Stanny L.A. (2006) Effects of different diets on juvenile tench, *Tinca tinca* (L.) reared under controlled conditions, *Aquaculture International*, *14*(1-2), 89-98.

Wood P.J. & Petts G.E. (1994) Low flows and recovery of macroinvertebrates in a small regulated chalk stream, *Regulated Rivers: Research & Management*, *9*(4), 303-316.

Wood P.J. & Armitage P.D. (1997) Biological effects of fine sediment in the lotic environment, *Environmental Management*, *21*(2), 203-217.

Wood P.J. & Armitage P.D. (2004) The response of the macroinvertebrate community to low-flow variability and supra-seasonal drought within a groundwater dominated stream, *Fundamental and Applied Limnology*, *161*(1), 1-20.

Wood P.J., Boulton A.J., Little S. & Stubbington R. (2010) Is the hyporheic zone a refugium for aquatic macroinvertebrates during severe low flow conditions?, *Fundamental and Applied Limnology*, *176*(4), 377-390.

Woodward G., Perkins D.M. & Brown L.E. (2010) Climate change and freshwater ecosystems: impacts across multiple levels of organization, *Philosophical Transactions of the Royal Society B: Biological Sciences*, *365*(1549), 2093-2106.

Worrall T.P., Dunbar M.J., Extence C.A., Laize C.L., Monk W.A. & Wood P.J. (2014) The identification of hydrological indices for the characterization of macroinvertebrate community response to flow regime variability, *Hydrological Sciences Journal*, *59*(3-4), 645-658.

Wright J.F. & Berrie A.D. (1987) Ecological effects of groundwater pumping and a natural drought on the upper reaches of a chalk stream*, Regulated Rivers: Research & Management, 1*(2), 145-160*.*

Wright J.F. & Symes K.L. (1999) A nine-year study of the macroinvertebrate fauna of a chalk stream, *Hydrological Processes*, *13*(3), 371-385.

WWF (2009) Rivers on the edge, Surry, UK.

WWF (2014) The state of England's chalk streams, Surry UK.

Xu C., Letcher B.H. & Nislow K.H. (2010) Context-specific influence of water temperature on Brook Trout growth rates in the field, *Freshwater Biology, 55*, 2253-2264.

Young M. (1994) Mobility of Brown Trout in southcentral Wyoming streams, *Canadian Journal of Zoology, 72*, 2078-2083.

Zhao Y., Xiong X., Wu C., Xia Y., Li J. & Wu Y. (2018) Influence of light and temperature on the development and denitrification potential of periphytic biofilms, *Science of The Total Environment*, *613*, 1430-1437.

Zippin C. (1956) An evaluation of the removal method of estimating animal populations, *Biometrics*, *12*(2), 163-189.

Appendix 1

Table A1.1: Taxa measurement and mass formula

Taxa	Source	Measurement	Formula	Source
Anisoptera lv.	Aquatic	Head width	EXP(((LN([BL]))*2.51)-0.46)	Smock (1980)
Anura	Terrestrial	Body length	(-0.6503 +(0.0735 * BL))	Denis & Jiménez (2009)
Aphididae	Terrestrial	Body length	EXP(((LN([BL]))*2.4)-3.461)	Smock (1980)
Arionidae	Terrestrial	Body length	(10^((1.8865*(LOG10([BL])))-1.2692))	R. Lauridsen unpubl. data
Asellus aquaticus	Aquatic	Largest dimension	(10^(([BL]*0.1934)-0.0302))/10	Mason (1997)
Baetidae lv.	Aquatic	Head width	EXP(((LN([BL]))*3.31)-0.44)	Burgherr & Meyer (1997)
Brachycentridae lv.	Aquatic	Head width	2.221*([BL]^3.349)	Benke *et al*. (1999)
Calopterygidae lv.	Aquatic	Body length	EXP(((LN([BL]))*2.51)-0.46)	Smock (1980)
Ceratopogonidae lv.	Aquatic	Body length	EXP((3.7948*LN([BL]))-9.3774)	Meyer (1989)
Chironomidae lv.	Aquatic	Body length	EXP((2.5*LN([BL]))-6.3)	Meyer (1989)
Cicadellidae ad.	Terrestrial	Body length	0.079*([BL]^2.229)	Sabo *et al*. (2002)
Cladocera	Aquatic	Largest dimension	(EXP((2.653*LN([BL]))+1.7512))/1000	Herzig (1974)
Collembola	Aquatic	Body length	0.05*([BL]^2.06)	Sabo *et al*. (2002)
Culicidae ad.	Terrestrial	Body length	0.032*([BL]^2.038)	Sabo *et al*. (2002)
Dermaptera	Terrestrial	Body length	(0.2037*[BL])+0.79319	Ganihar (1997)
Dicranota sp. lv	Aquatic	Body length	EXP(((LN([BL]))*1.91)-5.53)	Burgherr & Meyer (1997)
Diplopoda	Terrestrial	Body length	EXP(((LN([BL]))*2.1006)-3.2882)	Ganihar (1997)
Diptera pu.	Aquatic	Body length	EXP((2.24*LN([BL]))-5.26)	Meyer (1989)
Dixidae lv.	Aquatic	Body length	EXP((-5.9986+(2.5717*(LN([BL]))))))	Burgherr & Meyer (1997)
Dytiscidae	Aquatic	Body Length	0.04*([BL]^2.64)	Burgherr & Meyer (1997)
Elmis aenea ad.	Aquatic	Body length	EXP(((LN([BL]))*6.18)-6.98)	Burgherr & Meyer (1997)
Elmis aenea lv.	Aquatic	Body length	EXP(((LN([BL]))*3.099)-5.67)	Burgherr & Meyer (1997)
Empididae lv.	Aquatic	Body length	EXP((2.7288*LN([BL]))-5.3506)	Meyer (1989)
Ephemerellidae lv.	Aquatic	Head width	EXP(((LN([BL]))*3.5793)-0.5374)	Meyer (1989)

Table A1.1 continued

Taxa	Source	Measurement	Formula	Source
Ephemeridae lv.	Aquatic	Head width	EXP(((LN([BL]))*2.18)-0.88)	Burgherr & Meyer (1997)
Ephemeroptera ad.	Terrestrial	Body length	0.014*([BL]^2.49)	Sabo *et al*. (2002)
Ephydridae	Terrestrial	Body length	0.006*([BL]^3.05)	Sabo *et al*. (2002)
Fish	Aquatic	Body length	10^(((LOG10([BL]))*3.3292)-6.3775)*1000	Edwards *et al*. (2008)
Formicidae	Terrestrial	Body length	0.027*([BL]^2.666)	Sabo *et al*. (2002)
Gammarus pulex	Aquatic	Largest dimension	EXP((2.83*LN([BL]))-4.95)	Burgherr & Meyer (1997)
Gastropod	Aquatic/Terrestrial	Largest dimension	0.172*([BL]^1.688)	Benke *et al*. (1999)
Glossosomatidae lv.	Aquatic	Head width	EXP(((LN([BL]))*2.9789)+0.959)	Meyer (1989)
Goeridae lv.	Aquatic	Head width	EXP(((LN([BL]))*3.5755)+0.8613)	Meyer (1989)
Gyrinidae ad.	Aquatic	Body length	0.0077*([BL]^2.91)	Benke *et al*. (1999)
Haliplus sp. lv.	Aquatic	Body length	EXP((-4.4518+(2.4724*(LN([BL]))))))	Meyer (1989)
Heptageniidae lv.	Aquatic	Head width	EXP(((LN([BL]))*3.22)-2.16)	Burgherr & Meyer (1997)
Hirudinea	Aquatic	Body length	EXP((1.9977*LN([BL]))-2.1192)	Edwards *et al*. (2009)
Homoptera	Terrestrial	Body length	0.005*([BL]^3.33)	Sabo *et al*. (2002)
Hydracarina	Aquatic	Largest dimension	0.05*([BL]^2.74)	Sabo *et al*. (2002)
Hydrometridae ad.	Terrestrial	Body length	EXP(((LN([BL]))*2.4)-3.461)	Smock (1980)
Hydropsychidae lv.	Aquatic	Head width	EXP(((LN([BL]))*2.7343)+0.4011)	Meyer (1989)
Hydroptilidae lv.	Aquatic	Head width	EXP(((LN([BL]))*2.794EXP(((LN([BL]))*2.7343)+0.4011)6)-5.2867)	Meyer (1989)
Lepidoptera lv.	Terrestrial	Body length	0.012*([BL]^2.69)	Sabo *et al*. (2002)
Leptoceridae lv.	Aquatic	Head width	EXP(((LN([BL]))*2.7343)+0.4011)	Meyer (1989)
Leuctridae lv.	Aquatic	Head width	EXP(((LN([BL]))*3.13)-0.59)	Burgherr & Meyer (1997)
Limnephilidae lv.	Aquatic	Head width	EXP(((LN([BL]))*3.1678)+0.4109)	Meyer (1989)
Limnius volckmari ad.	Aquatic	Body length	EXP(((LN([BL]))*3.83)-4.89)	Burgherr & Meyer (1997)
Limnius volckmari lv.	Aquatic	Body length	EXP(((LN([BL]))*4.53)-8.71)	Burgherr & Meyer (1997)

Table A1.1 continued

Taxa	Source	Measurement	Formula	Source
Lumbricidae	Terrestrial	Body length	(10^((1.8865*(LOG10([BL])))-1.2692))	Edwards (1998)
Miridae	Terrestrial	Body length	EXP(((LN([BL]))*2.4)-3.461)	Smock (1980)
Mycetophilidae lv.	Terrestrial	Body length	EXP((-5.9986+(2.5717*(LN([BL])))))	Burgherr & Meyer (1997)
Nabidae	Terrestrial	Body length	EXP(((LN([BL]))*2.4)-3.461)	Smock (1980)
Notonectidae ad.	Aquatic	Body length	0.04*([BL]^2.64)	Burgherr & Meyer (1997)
Odontocerum albicorne lv.	Aquatic	Head width	EXP(((LN([BL]))*3.0393)+0.8007)	Meyer (1989)
Oligochaeta	Aquatic	Body length	(10^(((LOG10([BL]))*1.2059)-0.1751))/100	Mason (1977)
Pedicidae	Aquatic	Pedicia sp. lv.	EXP(((LN([BL]))*3.1059)-7.8392)	Meyer (1989)
Pentatomidae	Terrestrial	Body length	EXP(((LN([BL]))*2.4)-3.461)	Smock (1980)
Pisidium sp.	Aquatic	Largest dimension	([BL]^2.477)*0.0163	Benke *et al*. (1999)
Planariidae	Aquatic	Body length	([BL]^2.198)*0.0056	Benke *et al*. (1999)
Plecoptera ad.	Terrestrial	Body length	0.014*([BL]^2.49)	Sabo *et al*. (2002)
Polycentropodidae lv.	Aquatic	Head width	((10^(((LOG10([BL]))*2.8)+2.58)))/1000	Hildrew & Townsend (1982)
Psocids	Terrestrial	Body length	EXP(((LN([BL]))*2.4)-3.461)	Smock (1980)
Psychomyiidae lv.	Aquatic	Head width	EXP(((LN([BL]))*3.09)+0.7907)	Meyer (1989)
Rhyacophilidae lv.	Aquatic	Head width	EXP(((LN([BL]))*3.53)+0.69)	Burgherr & Meyer (1997)
Sericostomatidae lv.	Aquatic	Head width	EXP(((LN([BL]))*2.9153)+0.1692)	Meyer (1989)
Simuliidae lv.	Aquatic	Body length	EXP(((LN([BL]))*2.0742)-4.5009)	Meyer (1989)
Stratiomyidae lv.	Terrestrial	Body length	0.006*([BL]^3.05)	Sabo *et al*. (2002)
Syrphidae ad.	Terrestrial	Body length	0.006*([BL]^3.05)	Sabo *et al*. (2002)
Terrestrial araneae	Terrestrial	Body length	0.05*([BL]^2.74)	Sabo *et al*. (2002)
Terrestrial coleoptera ad.	Terrestrial	Body length	0.04*([BL]^2.64)	Sabo *et al*. (2002)
Terrestrial coleoptera lv.	Terrestrial	Body length	EXP((-4.4518+(2.4724*(LN([BL])))))	Meyer (1989)
Terrestrial diptera	Terrestrial	Body length	0.04*([BL]^2.26)	Sabo *et al*. (2002)

Table A1.1 continued

Taxa	Source	Measurement	Formula	Source
Thysanoptera ad.	Terrestrial	Body length	0.05*([BL]^2.06)	Sabo *et al*. (2002)
Tipulidae ad.	Terrestrial	Body length	0.1*([BL]^1.57)	Sabo *et al*. (2002)
Tipulidae lv.	Aquatic	Body length	([BL]^2.681)*0.0029	Benke *et al*. (1999)
Trichoptera ad.	Terrestrial	Body length	0.01*([BL]^2.9)	Sabo *et al*. (2002)
Trichoptera pu.	Aquatic	Head width	EXP(((LN([BL]))*2.7946)-5.2867)	Meyer (1989)
Veliidae	Terrestrial	Body length	EXP(((LN([BL]))*2.4)-3.461)	Smock (1980)

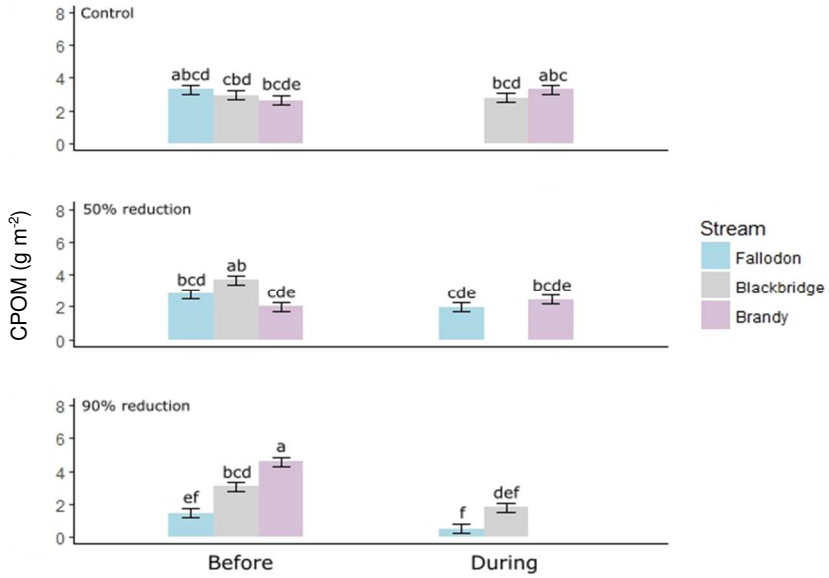

Figure A1.1: Mean (±standard error) CPOM standing stock showing effects of three different discharge treatments. Gaps occur where no data are available. Results of Tukey's post hoc comparisons shown, where mean values sharing the same letter are not significantly different.

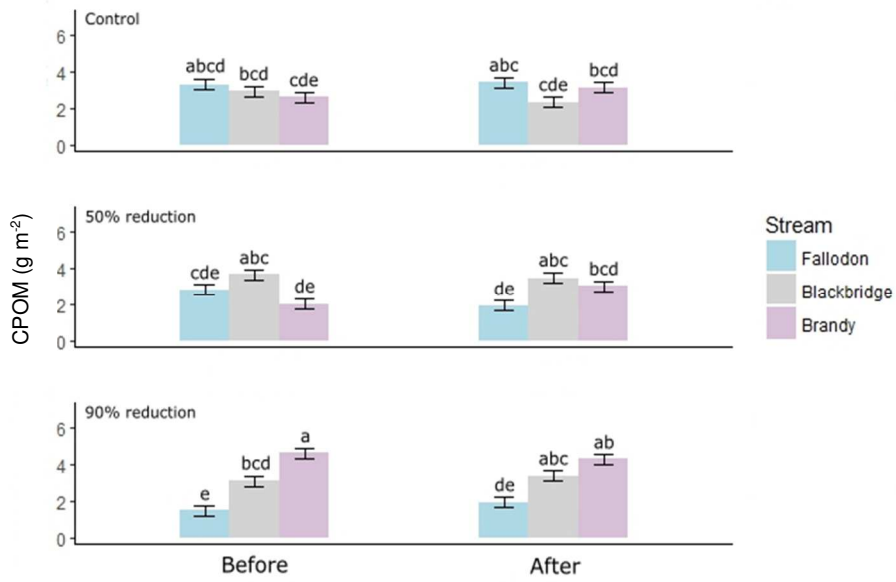

Figure A1.2: Mean (±standard error) CPOM standing stock showing lasting effects of the three different discharge treatments. Results of Tukey's post hoc comparisons shown, where mean values sharing the same letter are not significantly different.

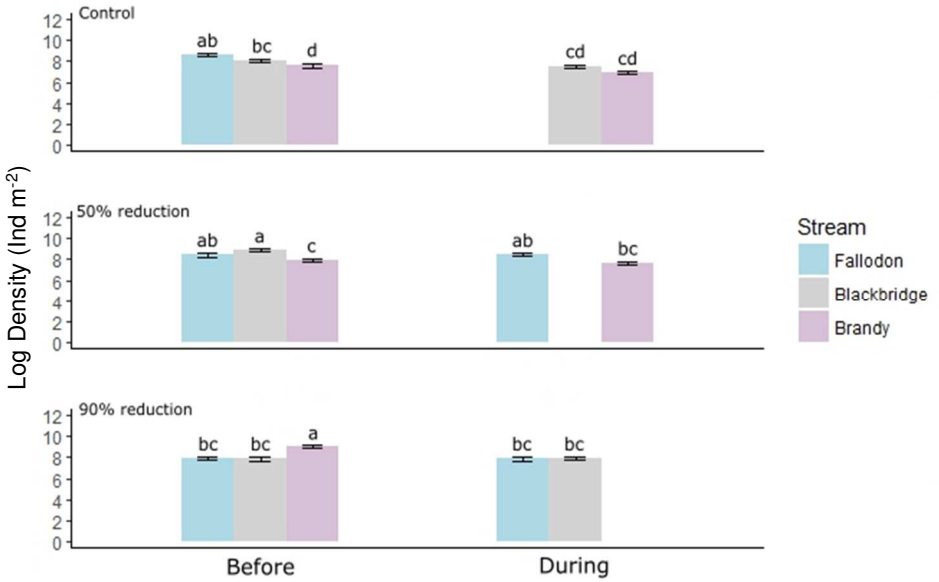

Figure A1.3: Mean (±standard error) (log) macroinvertebrate density showing effects of three different discharge treatments. Gaps occur where no data are available. Results of Tukey's post hoc comparisons shown, where mean values sharing the same letter are not significantly different.

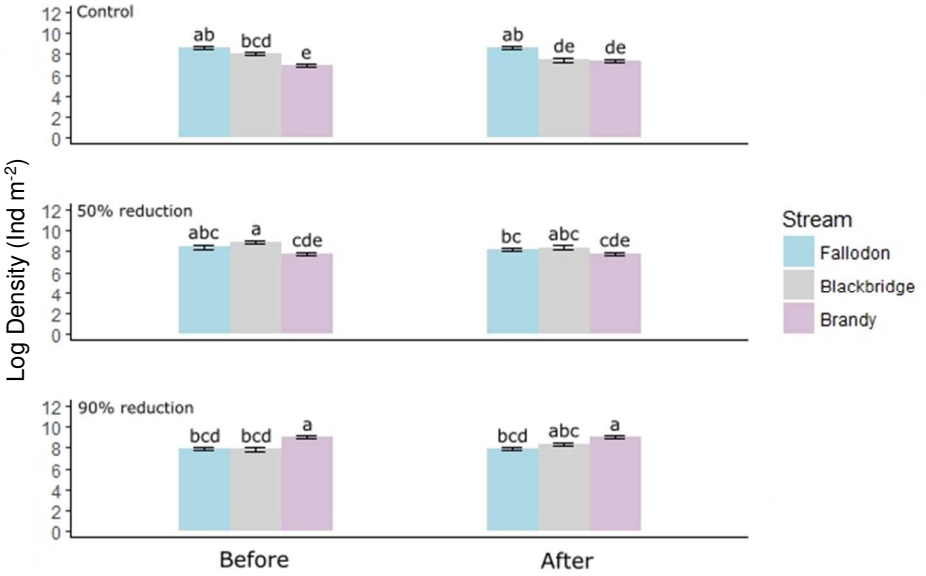

Figure A1.4: Mean (±standard error) (log) macroinvertebrate density showing lasting effects of the three different discharge treatments. Results of Tukey's post hoc comparisons shown, where mean values sharing the same letter are not significantly different.

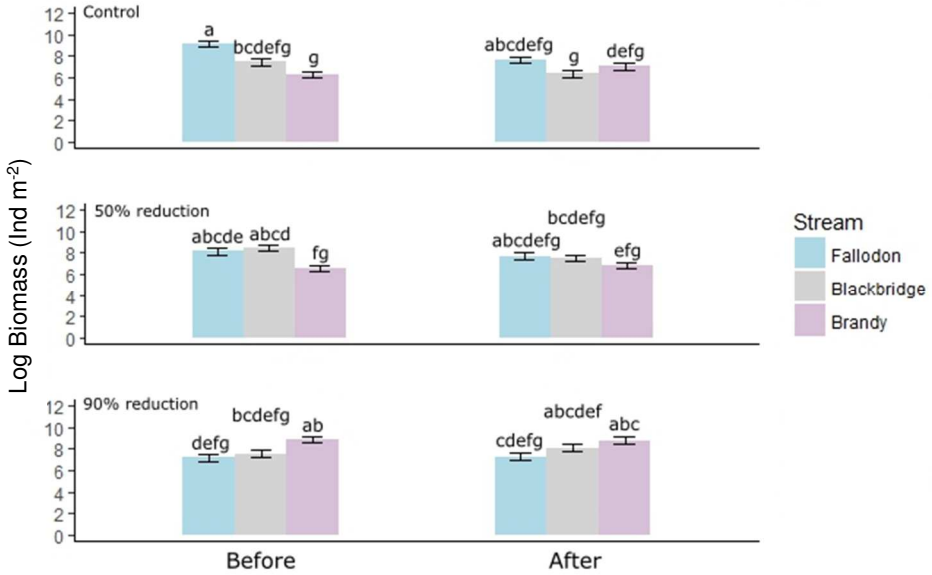

Figure A1.5: Mean (±standard error) (log) macroinvertebrate biomass showing lasting effects of the three different discharge treatments. Results of Tukey's post hoc comparisons shown, where mean values sharing the same letter are not significantly different.

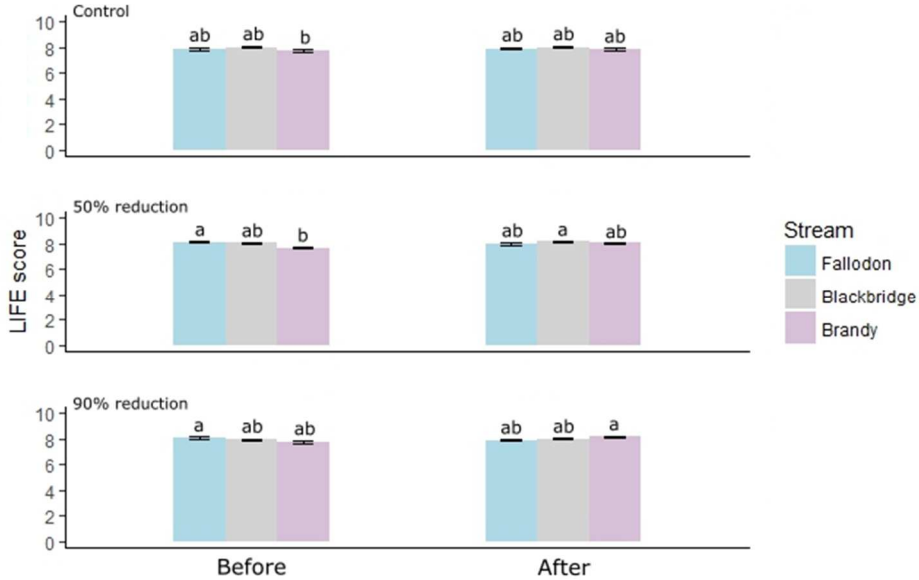

Figure A1.6: Mean (±standard error) LIFE score showing lasting effects of the three different discharge treatments. Results of Tukey's post hoc comparisons shown, where mean values sharing the same letter are not significantly different.

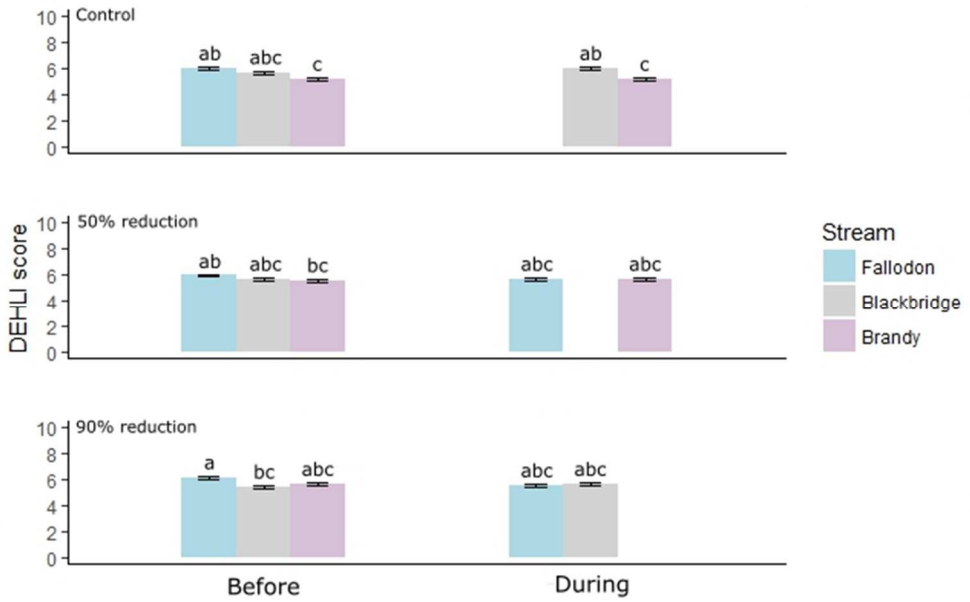

Figure A1.7: Mean (±standard error) DEHLI score showing effects of three different discharge treatments. Gaps occur where no data is available. Results of Tukey's post hoc comparisons shown, where mean values sharing the same letter are not significantly different.

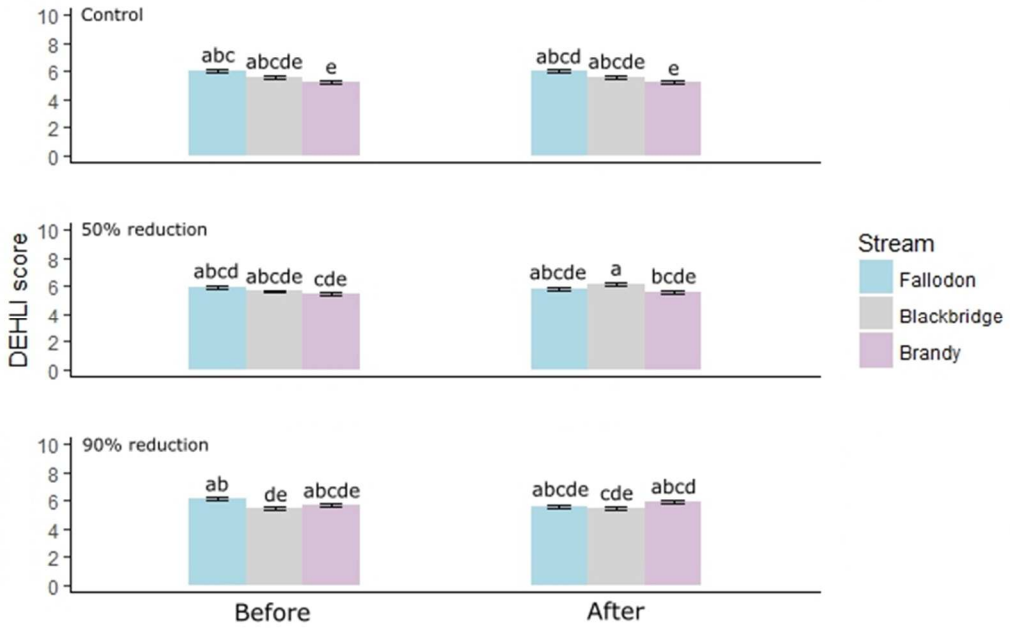

Figure A1.8: Mean (±standard error) DEHLI score showing lasting effects of the three different discharge treatments. Results of Tukey's post hoc comparisons shown, where mean values sharing the same letter are not significantly different.

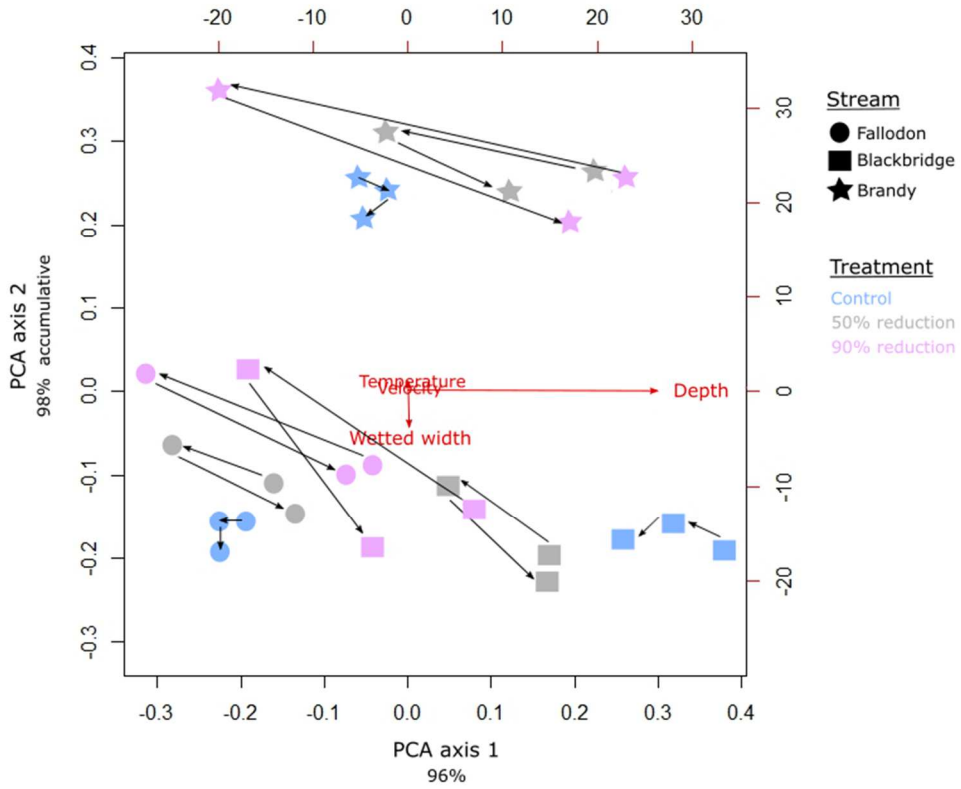

Figure A1.9: Principle Component Analysis (PCA) plot showing variation among streams and treatments in terms of environmental variables (depth, velocity, temperature and wetted width) over the experimental period. Vectors (red) indicate the direction of change over time and strength of contribution of each environmental variable to the overall distribution. Symbols represent different streams, colours represent different treatments and arrows show direction of change between sampling occasions defined within this study. The first principle axis explained 96% of the variation with an additional 2% explained by the second principle axis.

Table A1.2: Statistical results of GLM testing relationship between axis 1 PC scores and macroinvertebrate univariate variables. LIFE = Lotic-invertebrate index for flow evaluation, DEHLI = Drought effect of habitat loss on invertebrates, ASPT = average score per taxon.

Univariate response	Source	df	est	se	Z	*p*
Density (ind m^{-2})	Intercept		2.088	.022	91.555	***
	Axis 1 PC score	1	-.0001	.003	-.038	
Biomass (g m^{-2})	Intercept		2.018	.023	85.514	***
	Axis 1 PC score	1	-.003	.003	-.865	
LIFE	Intercept		7.285	4.50	16.18	***
	Axis 1 PC score	1	2.94	6.97	.004	
DEHLI	Intercept		5.512	4.918	11.207	***
	Axis 1 PC score	1	-4.781	7.626	-.006	
ASPT	Intercept		.5584	.0489	11.397	***
	Axis 1 PC score	1	-.0002	.0075	-.036	

Table A1.3: List of taxa abbreviations from Figure 2.13.

Scientific name	Taxa abbreviation	Scientific name	Taxa abbreviation
Ancylus fluviatilis	*Ancylus*	*Hydroptila sp.*	*Hydropti*
Anotcha vitripennis	*Anotcha*	*Hydropsyche siltalai*	*Hydrops*
Baetis rhodani	*Baetis r*	*Leuctra moselyi*	*Leuct*
Baetis scambus	*Baetis s*	*Limnius volckmari*	*Limnius*
Caenis luctosa	*Caenis*	*Lumbricidae*	*Lumbri*
Ceratopogonidae	*Cerato*	*Odontocerum albicorne*	*Odont*
Chaetopteryx villosa	*Chae*	*Oligochaeta*	*Oligo*
Chelifera	*Chelif*	*Polycelis feline*	*Polycelis f*
Chironomidae	*Chiro*	*Polycelis tenuis*	*Polycelis t*
Dicranota	*Dicra*	*Potamopyrgus antipodarium*	*Potam*
Diptera lv	*Diptera*	*Psychomyia pusila*	*Psycho*
Elmis anea	*Elmis*	*Rhyacophila dorsalis*	*Rhyaco*
Ephemera Danica	*Ephem*	*Riolus subiolaceus*	*Riolus*
Gammarus group	*Gamm*	*Sericostoma personatum*	*Serico*
Glossiphonia complanta	*Glossi*	*Serratella ignita*	*Serra*
Glossosoma	*Glosso*	*Simulium*	*Simu*
Heptagenia sulphurea	*Heptag*	*Wiedemannia*	*Wiede*
Hydracarina	*Hydra*		

Appendix 2

Table A2.1: Taxa measurement and mass formula

Taxa	Source	Measurement	Formula	Source
Anisoptera lv.	Aquatic	Head width	EXP(((LN([BL]))*2.51)-0.46)	Smock (1980)
Anura	Terrestrial	Body length	(-0.6503 +(0.0735 * BL))	Denis & Jiménez (2009)
Aphididae	Terrestrial	Body length	EXP(((LN([BL]))*2.4)-3.461)	Smock (1980)
Arionidae	Terrestrial	Body length	(10^((1.8865*(LOG10([BL])))-1.2692))	R. Lauridsen unpubl. data
Asellus aquaticus	Aquatic	Largest dimension	(10^(([BL]*0.1934)-0.0302))/10	Mason (1997)
Baetidae lv.	Aquatic	Head width	EXP(((LN([BL]))*3.31)-0.44)	Burgherr & Meyer (1997)
Brachycentridae lv.	Aquatic	Head width	2.221*([BL]^3.349)	Benke *et al*. (1999)
Calopterygidae lv.	Aquatic	Body length	EXP(((LN([BL]))*2.51)-0.46)	Smock (1980)
Ceratopogonidae lv.	Aquatic	Body length	EXP((3.7948*LN([BL]))-9.3774)	Meyer (1989)
Chironomidae lv.	Aquatic	Body length	EXP((2.5*LN([BL]))-6.3)	Meyer (1989)
Cicadellidae ad.	Terrestrial	Body length	0.079*([BL]^2.229)	Sabo *et al*. (2002)
Cladocera	Aquatic	Largest dimension	(EXP((2.653*LN([BL]))+1.7512))/1000	Herzig (1974)
Collembola	Aquatic	Body length	0.05*([BL]^2.06)	Sabo *et al*. (2002)
Culicidae ad.	Terrestrial	Body length	0.032*([BL]^2.038)	Sabo *et al*. (2002)
Dermaptera	Terrestrial	Body length	(0.2037*[BL])+0.79319	Ganihar (1997)
Dicranota sp. lv	Aquatic	Body length	EXP(((LN([BL]))*1.91)-5.53)	Burgherr & Meyer (1997)
Diplopoda	Terrestrial	Body length	EXP(((LN([BL]))*2.1006)-3.2882)	Ganihar (1997)
Diptera pu.	Aquatic	Body length	EXP((2.24*LN([BL]))-5.26)	Meyer (1989)
Dixidae lv.	Aquatic	Body length	EXP((-5.9986+(2.5717*(LN([BL]))))))	Burgherr & Meyer (1997)
Dytiscidae	Aquatic	Body Length	0.04*([BL]^2.64)	Burgherr & Meyer (1997)
Elmis aenea ad.	Aquatic	Body length	EXP(((LN([BL]))*6.18)-6.98)	Burgherr & Meyer (1997)
Elmis aenea lv.	Aquatic	Body length	EXP(((LN([BL]))*3.099)-5.67)	Burgherr & Meyer (1997)
Empididae lv.	Aquatic	Body length	EXP((2.7288*LN([BL]))-5.3506)	Meyer (1989)
Ephemerellidae lv.	Aquatic	Head width	EXP(((LN([BL]))*3.5793)-0.5374)	Meyer (1989)

Table A2.1 continued

Taxa	Source	Measurement	Formula	Source
Ephemeridae lv.	Aquatic	Head width	EXP(((LN([BL]))*2.18)-0.88)	Burgherr & Meyer (1997)
Ephemeroptera ad.	Terrestrial	Body length	0.014*([BL]^2.49)	Sabo *et al*. (2002)
Ephydridae	Terrestrial	Body length	0.006*([BL]^3.05)	Sabo *et al*. (2002)
Fish	Aquatic	Body length	10^(((LOG10([BL]))*3.3292)-6.3775)*1000	Edwards *et al*. (2008)
Formicidae	Terrestrial	Body length	0.027*([BL]^2.666)	Sabo *et al*. (2002)
Gammarus pulex	Aquatic	Largest dimension	EXP((2.83*LN([BL]))-4.95)	Burgherr & Meyer (1997)
Gastropod	Aquatic/Terrestrial	Largest dimension	0.172*([BL]^1.688)	Benke *et al*. (1999)
Glossosomatidae lv.	Aquatic	Head width	EXP(((LN([BL]))*2.9789)+0.959)	Meyer (1989)
Goeridae lv.	Aquatic	Head width	EXP(((LN([BL]))*3.5755)+0.8613)	Meyer (1989)
Gyrinidae ad.	Aquatic	Body length	0.0077*([BL]^2.91)	Benke *et al*. (1999)
Haliplus sp. lv.	Aquatic	Body length	EXP((-4.4518+(2.4724*(LN([BL]))))))	Meyer (1989)
Heptageniidae lv.	Aquatic	Head width	EXP(((LN([BL]))*3.22)-2.16)	Burgherr & Meyer (1997)
Hirudinea	Aquatic	Body length	EXP((1.9977*LN([BL]))-2.1192)	Edwards *et al*. (2009)
Homoptera	Terrestrial	Body length	0.005*([BL]^3.33)	Sabo *et al*. (2002)
Hydracarina	Aquatic	Largest dimension	0.05*([BL]^2.74)	Sabo *et al*. (2002)
Hydrometridae ad.	Terrestrial	Body length	EXP(((LN([BL]))*2.4)-3.461)	Smock (1980)
Hydropsychidae lv.	Aquatic	Head width	EXP(((LN([BL]))*2.7343)+0.4011)	Meyer (1989)
Hydroptilidae lv.	Aquatic	Head width	EXP(((LN([BL]))*2.794EXP(((LN([BL]))*2.7343)+0.4011)6)-5.2867)	Meyer (1989)
Lepidoptera lv.	Terrestrial	Body length	0.012*([BL]^2.69)	Sabo *et al*. (2002)
Leptoceridae lv.	Aquatic	Head width	EXP(((LN([BL]))*2.7343)+0.4011)	Meyer (1989)
Leuctridae lv.	Aquatic	Head width	EXP(((LN([BL]))*3.13)-0.59)	Burgherr & Meyer (1997)
Limnephilidae lv.	Aquatic	Head width	EXP(((LN([BL]))*3.1678)+0.4109)	Meyer (1989)
Limnius volckmari ad.	Aquatic	Body length	EXP(((LN([BL]))*3.83)-4.89)	Burgherr & Meyer (1997)
Limnius volckmari lv.	Aquatic	Body length	EXP(((LN([BL]))*4.53)-8.71)	Burgherr & Meyer (1997)

Table A2.1 continued

Taxa	Source	Measurement	Formula	Source
Lumbricidae	Terrestrial	Body length	(10^((1.8865*(LOG10([BL])))-1.2692))	Edwards (1998)
Miridae	Terrestrial	Body length	EXP(((LN([BL]))*2.4)-3.461)	Smock (1980)
Mycetophilidae lv.	Terrestrial	Body length	EXP((-5.9986+(2.5717*(LN([BL])))))	Burgherr & Meyer (1997)
Nabidae	Terrestrial	Body length	EXP(((LN([BL]))*2.4)-3.461)	Smock (1980)
Notonectidae ad.	Aquatic	Body length	0.04*([BL]^2.64)	Burgherr & Meyer (1997)
Odontocerum albicorne lv.	Aquatic	Head width	EXP(((LN([BL]))*3.0393)+0.8007)	Meyer (1989)
Oligochaeta	Aquatic	Body length	(10^(((LOG10([BL]))*1.2059)-0.1751))/100	Mason (1977)
Pedicidae	Aquatic	Pedicia sp. lv.	EXP(((LN([BL]))*3.1059)-7.8392)	Meyer (1989)
Pentatomidae	Terrestrial	Body length	EXP(((LN([BL]))*2.4)-3.461)	Smock (1980)
Pisidium sp.	Aquatic	Largest dimension	([BL]^2.477)*0.0163	Benke *et al*. (1999)
Planariidae	Aquatic	Body length	([BL]^2.198)*0.0056	Benke *et al*. (1999)
Plecoptera ad.	Terrestrial	Body length	0.014*([BL]^2.49)	Sabo *et al*. (2002)
Polycentropodidae lv.	Aquatic	Head width	((10^(((LOG10([BL]))*2.8)+2.58)))/1000	Hildrew & Townsend (1982)
Psocids	Terrestrial	Body length	EXP(((LN([BL]))*2.4)-3.461)	Smock (1980)
Psychomyiidae lv.	Aquatic	Head width	EXP(((LN([BL]))*3.09)+0.7907)	Meyer (1989)
Rhyacophilidae lv.	Aquatic	Head width	EXP(((LN([BL]))*3.53)+0.69)	Burgherr & Meyer (1997)
Sericostomatidae lv.	Aquatic	Head width	EXP(((LN([BL]))*2.9153)+0.1692)	Meyer (1989)
Simuliidae lv.	Aquatic	Body length	EXP(((LN([BL]))*2.0742)-4.5009)	Meyer (1989)
Stratiomyidae lv.	Terrestrial	Body length	0.006*([BL]^3.05)	Sabo *et al*. (2002)
Syrphidae ad.	Terrestrial	Body length	0.006*([BL]^3.05)	Sabo *et al*. (2002)
Terrestrial araneae	Terrestrial	Body length	0.05*([BL]^2.74)	Sabo *et al*. (2002)
Terrestrial coleoptera ad.	Terrestrial	Body length	0.04*([BL]^2.64)	Sabo *et al*. (2002)
Terrestrial coleoptera lv.	Terrestrial	Body length	EXP((-4.4518+(2.4724*(LN([BL])))))	Meyer (1989)
Terrestrial diptera	Terrestrial	Body length	0.04*([BL]^2.26)	Sabo *et al*. (2002)

Table A2.1 continued

Taxa	Source	Measurement	Formula	Source
Thysanoptera ad.	Terrestrial	Body length	0.05*([BL]^2.06)	Sabo *et al*. (2002)
Tipulidae ad.	Terrestrial	Body length	0.1*([BL]^1.57)	Sabo *et al*. (2002)
Tipulidae lv.	Aquatic	Body length	([BL]^2.681)*0.0029	Benke *et al*. (1999)
Trichoptera ad.	Terrestrial	Body length	0.01*([BL]^2.9)	Sabo *et al*. (2002)
Trichoptera pu.	Aquatic	Head width	EXP(((LN([BL]))*2.7946)-5.2867)	Meyer (1989)
Veliidae	Terrestrial	Body length	EXP(((LN([BL]))*2.4)-3.461)	Smock (1980)

Table A2.2: Statistical results of ANOVA testing the effects of different discharge treatments (within the During sampling occasion) on macroinvertebrate total/aquatic/terrestrial abundance and biomass delivery rate.

	Total					Aquatic					Terrestrial				
Source	**df**	**ss**	**ms**	**F**	***p***	**df**	**ss**	**ms**	**F**	***P***	**df**	**ss**	**ms**	**F**	***p***
Abundance															
Year	2	11.94	5.97	7.17	**	2	12.77	6.38	8.19	**	2	.001	.0019	1.71	
Treatment	2	3.02	1.51	1.81		2	2.78	1.39	1.78		2	.002	.0013	1.13	
Stream	2	7.75	3.87	4.66	*	2	6.59	3.29	4.23	*	2	.002	.0013	1.13	
Treatment:Stream	4	.73	.36	0.44		4	0.71	.35	0.45		4	.003	.0011	.94	
Residuals	25	22.46	.83			25	21.02	.77			25	.031	.0012		
Biomass															
Year	2	.010	.010	1.56		2	.0003	.0004	1.48		2	.007	.007	1.56	
Treatment	2	.012	.006	.04		2	.0002	.0001	.58		2	.008	.004	1.03	
Stream	2	.015	.007	1.12		2	.0007	.0004	1.45		2	.008	.004	1.03	
Treatment:Stream	4	.014	.005	0.72		4	.0003	.0001	.41		4	.011	.003	0.86	
Residuals	25	.176	,007			25	.0067	.0002			25	.115	.004		

****p <0.001, **p <0.01, *p <0.05*, Blanks = *p >0.05*.

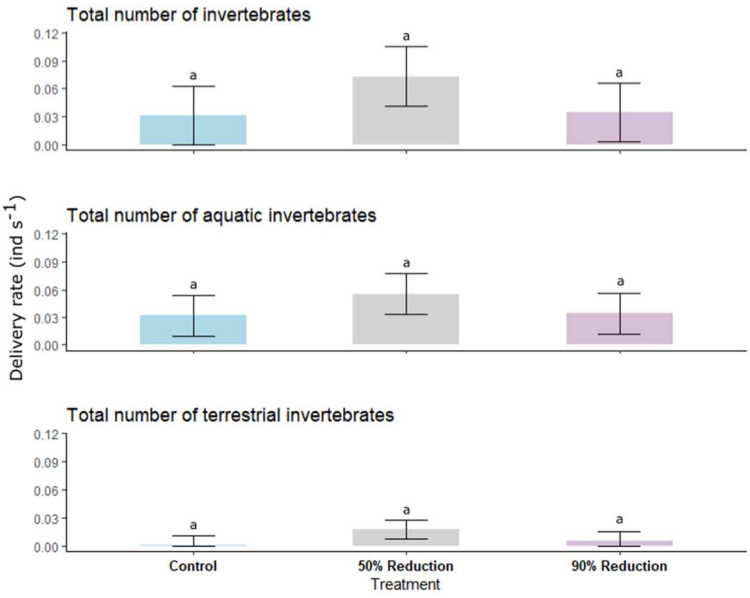

Figure A2.1: The effect of experimental discharge reduction on mean (± standard error) delivery rate of individuals (total/aquatic/terrestrial) within the During occasion. Results of Tukey's post hoc comparisons shown: mean values sharing the same letter are not significantly different.

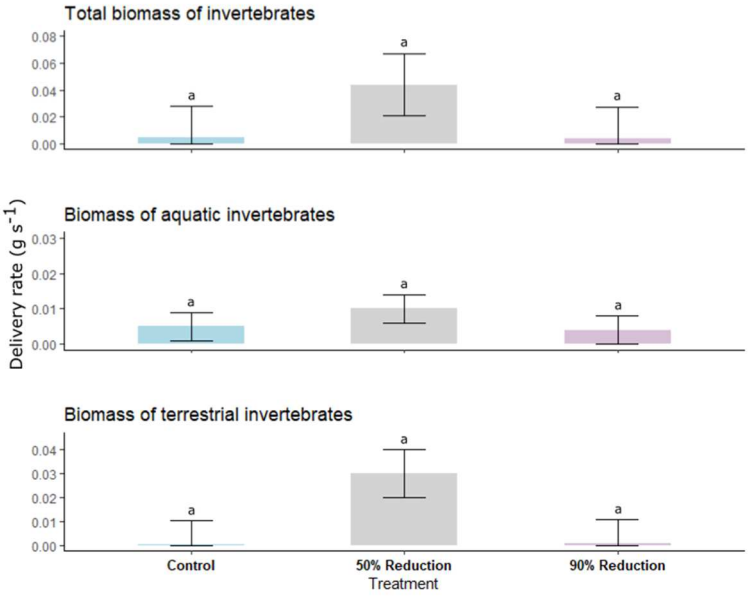

Figure A2.2: The effect of experimental discharge reduction on mean (± standard error) delivery rate of biomass (total/aquatic/terrestrial) within the During occasion. Results of Tukey's post hoc comparisons shown: mean values sharing the same letter are not significantly different. Note: different y axis.

Table A2.3: Statistical results of ANOVA testing stream effects of reduced discharge on salmonid diet.

	Abundance					Richness					Total biomass					Proportion of terrestrial biomass				
Source	**df**	**ss**	**ms**	**F**	***p***	**Df**	**ss**	**ms**	**F**	***P***	**df**	**ss**	**ms**	**F**	***p***	**df**	**ss**	**ms**	**F**	***p***
Salmon																				
Year	2	10.77	5.39	4.19	*	2	3.01	1.50	4.41	*	2	17.86	8.93	3.26	*	2	.005	.002	1.25	
Treatment	2	42.50	21.25	16.54	***	2	1.28	.64	1.88		2	18.50	9.25	3.38	*	2	.001	.001	.32	
Occasion	1	39.96	39.96	31.11	***	1	.39	.39	1.15		1	52.64	52.63	19.2	***	1	.005	.005	2.44	
Stream	2	16.13	8.06	6.28	**	2	.35	.17	.52		2	34.59	17.29	6.32	**	2	.008	.004	1.84	
Treatment:Occasion:Stream	10	133.82	13.38	10.41	***	10	4.49	.44	1.32		10	218.92	21.89	8.01	***	10	.006	.002	1.49	
Residuals	226	290.27	1.28			226	76.89	.34			226	615.32	2.73			226	.518	.002		
0+ trout																				
Year	2	6.41	3.20	4.27	*	2	5.25	2.62	8.97	***	2	7.65	3.82	1.76		2	.003	.0019	5.84	**
Treatment	2	1.61	.80	1.07		2	2.52	1.25	4.29	*	2	4.48	2.42	1.11		2	.001	.0006	2.05	
Occasion	1	4.81	4.81	6.40	*	1	.14	.14	.50		1	56.49	56.48	26.0	***	1	.004	.0047	14.59	***
Stream	2	8.78	4.39	5.84	**	2	5.34	2.67	9.11	***	2	1.84	0.92	.42		2	.002	.0011	3.45	*
Treatment:Occasion:Stream	10	7.49	.74	.99		10	6.86	.68	2.34	*	10	83.52	8.35	3.85	***	10	.003	.0003	1.13	
Residuals	400	300.33	.75			400	117.21	.29			400	863.07	2.16			400	.130	.0003		
1+ trout																				
Year	2	6.14	3.07	4.24	*	2	7.17	3.58	10.95	***	2	49.54	24.77	6.09	**	2	.0031	.0015	2.88	
Treatment	2	.87	.43	.60		2	.89	.44	1.36		2	5.94	2.96	.73		2	.0015	.0007	1.45	
Occasion	1	.14	.14	.20		1	.20	.20	.63		1	54.68	54.68	13.4	***	1	.0148	.0148	27.42	***
Stream	2	12.08	6.04	8.34	***	2	3.91	1.95	5.97	**	2	11.76	5.87	1.44		2	.0003	.0001	.31	
Treatment:Occasion:Stream	10	32.34	3.23	4.46	***	10	8.28	.82	2.53	**	10	117.40	11.74	2.88	**	10	.0257	.0025	4.75	***
Residuals	386	279.73	.72			386	126.41	.32			386	1561.3	4.06			386	.2079	.0005		
≥2+ trout																				
Year	2	2.98	1.49	2.30		2	3.65	1.82	5.33	**	2	50.79	25.39	5.14	**	2	.18	.09	1.98	
Treatment	2	8.31	4.15	6.41	**	2	1.20	.60	1.76		2	62.40	31.2	6.32	**	2	.18	.09	1.94	
Occasion	1	.05	.05	.08		1	1.05	1.05	3.07		1	44.17	44.16	8.95	**	1	.38	.38	8.24	**
Stream	2	16.76	8.38	12.9	***	2	3.16	1.58	4.61	*	2	52.08	26.04	5.27	**	2	.42	.21	4.52	*
Treatment:Occasion:Stream	10	14.86	1.48	2.29		10	4.65	.46	1.35		10	168.90	16.89	3.42	***	10	1.24	.13	2.97	**
Residuals	214	138.76	.64			214	73.34	.34			214	1041	4.93			214	9.78	.04		

****p <0.001, **p <0.01, *p <0.05*, Blanks = *p >0.05*.

Table A2.4: Statistical results of ANOVA testing lasting stream effects of discharge reduction on salmonid diet.

	Abundance					Richness					Total biomass					Proportion of terrestrial biomass				
Source	**df**	**ss**	**ms**	**F**	***p***	**Df**	**ss**	**ms**	**F**	***P***	**df**	**ss**	**ms**	**F**	***p***	**df**	**ss**	**ms**	**F**	***p***
Salmon																				
Year	2	40.40	20.20	13.41	***	2	2.40	1.20	4.04	*	2	.79	.39	.17		2	.004	.002	.80	
Treatment	2	10.35	5.17	3.43	*	2	2.82	1.14	4.75	**	2	11.19	5.59	2.47		2	.005	.002	1.07	
Occasion	1	140.06	140.05	93.03	***	1	1.42	1.42	4.79	*	1	53.92	53.92	23.9	***	1	.001	.001	.40	
Stream	2	36.62	18.31	12.16	***	2	3.28	1.64	5.52	**	2	40.33	20.16	8.93	***	2	.013	.006	2.72	
Treatment:Occasion:Stream	10	159.42	15.94	10.58	***	10	2.79	.27	0.93		10	151.87	15.18	6.72	***	10	.012	.004	1.95	
Residuals	254	382.39	1.50			254	75.62	.29			254	573.37	2.25			254	.632	.002		
0+ trout																				
Year	2	6.31	3.15	4.31	*	2	5.90	2.95	11.34	***	2	1.71	.85	.42		2	.0029	.0014	6.63	**
Treatment	2	1.55	.77	1.06		2	2.94	1.47	5.65	**	2	20.74	10.36	5.18	**	2	.0006	.0003	1.53	
Occasion	1	5.52	5.52	7.55	**	1	1.97	1.97	7.58	**	1	3.82	3.81	1.90		1	.0005	.0005	2.49	
Stream	2	12.70	6.35	8.69	***	2	5.68	2.84	10.92	***	2	21.59	10.79	5.39	**	2	.0010	.0005	2.24	
Treatment:Occasion:Stream	10	14.10	1.41	1.92	*	10	9.38	.93	3.60	***	10	52.27	5.22	2.61	**	10	.0011	.0001	.50	
Residuals	410	299.67	.73			410	106.65	.26			410	814.18	2.00			410	.0909	.0002		
1+ trout																				
Year	2	9.55	4.77	6.15	**	2	5.92	2.96	8.32	***	2	30.52	15.26	4.00	*	2	.0139	.0069	14.22	***
Treatment	2	1.92	.96	1.24		2	1.49	.74	2.10		2	20.27	10.13	2.65		2	.0011	.0005	1.21	
Occasion	1	3.64	3.64	4.69	*	1	.34	.34	.97		1	74.11	74.10	19.4	***	1	.0035	.0035	7.25	**
Stream	2	14.35	7.17	9.25	**	2	2.48	1.24	3.49	*	2	7.45	3.72	.97		2	.0006	.0003	.63	
Treatment:Occasion:Stream	10	16.30	1.63	2.10	*	10	4.43	.44	1.24		10	69.63	6.96	1.82		10	.0067	.0006	1.36	
Residuals	401	311.16	.77			401	142.56	.35			401	1521.3	3.81			401	.1961	.0004		
≥2+ trout																				
Year	2	7.39	3.69	5.59	**	2	4.40	2.20	6.67	**	2	100.87	50.43	12.5	***	2	.13	.06	1.89	
Treatment	2	9.40	4.70	7.11	**	2	3.85	1.92	5.84	**	2	54.91	27.46	6.81	**	2	.33	.16	4.70	**
Occasion	1	1.41	1.41	2.14		1	4.25	4.25	12.8	***	1	4.16	4.15	1.03		1	.25	.25	7.25	**
Stream	2	8.21	4.10	6.21	**	2	3.20	1.60	4.85	**	2	5.84	2.92	.72		2	.39	.19	5.57	**
Treatment:Occasion:Stream	10	15.61	1.56	2.36	*	10	7.42	.74	2.24	*	10	168.77	16.97	4.21	***	10	2.27	.22	6.40	***
Residuals	230	151.97	.66			230	75.92	.33			230	910.29	4.02			230	8.02	.03		

****p <0.001, **p <0.01, *p <0.05*, Blanks = *p >0.05*.

Table A2.5: Statistical results of ANOVA testing for the effect of stream and a) reduced discharge and b) lasting effects of reduced discharge on the consumption rate of salmonids.

	a) Effects of reduced discharge										b) Lasting effects									
	Consumption rate (ind day^{-1})					Consumption rate (mg day^{-1})					Consumption rate (ind day^{-1})					Consumption rate (mg day^{-1})				
Source	df	ss	ms	F	*p*	df	ss	ms	F	*p*	df	ss	ms	F	*p*	df	ss	ms	F	*p*
Salmon																				
Year	2	4.16	2.08	3.4	*	2	24.89	12.45	5.79	**	2	3.67	1.83	3.07	*	2	13.69	6.84	4.09	*
Treatment	2	1.66	.83	1.36		2	4.72	2.35	1.09		2	2.53	1.26	2.12		2	15.11	7.55	4.51	*
Occasion	1	4.92	4.92	8.05	**	1	18.04	10.03	8.39	**	1	5.24	5.24	8.78	**	1	.03	.02	.01	
Stream	2	4.7	2.34	3.85	*	2	1.68	.84	.39		2	20.05	10	16.79	***	2	8.98	4.48	2.68	
Treatment:Occasion:Stream	10	19.83	1.98	3.24	***	10	57.98	5.79	2.69	**	10	11.53	1.15	1.93	*	10	27.06	2.7	1.61	
Residuals	233	142.29	.61			233	500.41	2.14			262	156.47	.59			262	438.06	1.67		
0+ trout																				
Year	2	15.72	7.86	12.7	***	2	9.78	4.89	2.39		2	16.28	8.14	13.59	***	2	43.33	21.66	11.51	***
Treatment	2	3.35	1.67	2.71		2	4.28	2.14	1.04		2	3.78	1.89	3.15	*	2	24.44	12.21	6.49	**
Occasion	1	3.74	3.74	6.04	*	1	2.95	2.95	1.44		1	1.18	1.18	1.97		1	3.46	3.46	1.83	
Stream	2	2.27	3.63	5.88	**	2	13.19	6.59	3.23	*	2	12.22	6.11	10.2	***	2	9.83	4.91	2.61	
Treatment:Occasion:Stream	10	7.47	.74	1.2		10	77.75	7.77	3.81	***	10	15.58	1.55	2.6	**	10	17.13	1.71	.91	
Residuals	488	301.92	.61			488	995.41	2.03			497	297.68	.59			497	935.45	1.88		
1+ trout																				
Year	2	5.01	2.5	4.07	*	2	18.3	9.15	2.28		2	.51	.25	.38		2	7.69	3.84	1.05	
Treatment	2	5.36	2.68	4.36	*	2	13.21	6.6	1.64		2	4.94	2.47	3.73	*	2	20.15	10.07	2.77	
Occasion	1	1.93	1.93	3.14		1	21.28	21.27	5.31	*	1	18.8	18.8	28.42	***	1	36.56	36.56	10.05	**
Stream	2	12.49	6.24	10.15	***	2	2.31	1.15	.28		2	16.13	8.06	12.19	***	2	.24	.12	.03	
Treatment:Occasion:Stream	10	35.03	3.05	5.69	***	10	31.63	3.16	.79		10	16.03	1.6	2.42	**	10	17.8	1.78	.48	
Residuals	444	273.18	.06			444	1776	4			459	303	.66			459	1668	3.63		
≥2+ trout																				
Year	2	.99	.49	.85		2	22.21	11.1	2.25		2	1.68	.83	1.45		2	36.4	18.2	4.51	*
Treatment	2	3.48	1.74	3		2	31.89	15.94	3.23	*	2	6.06	3.03	5.26	**	2	16.95	8.47	2.1	
Occasion	1	.38	.38	.65		1	13.09	13.09	2.65		1	.23	.23	.41		1	5.29	5.29	1.31	
Stream	2	12.51	6.25	10.77	***	2	29.65	14.82	3		2	6.03	3.01	5.23	**	2	24.35	12.17	3.02	
Treatment:Occasion:Stream	9	13005	1.45	2.49	*	9	86.21	9.57	1.94	*	10	14.46	1.44	2.5	**	10	115.75	11.57	2.87	**
Residuals	211	122.58	.58			211	1041	4.93			266	130.31	.57			226	910.29	4.02		

****p <0.001, **p <0.01, *p <0.05*, Blanks = *p >0.05*.

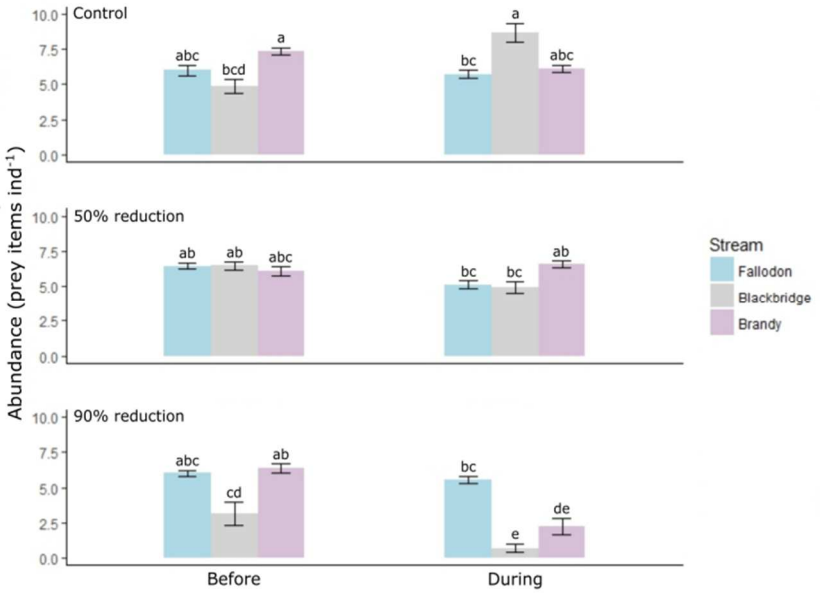

Figure A2.3: Influence of stream and experimental discharge reduction on mean abundance (± standard error) of prey in the guts of salmon. Results of Tukey's post hoc comparisons shown where mean values sharing the same letter are not significantly different.

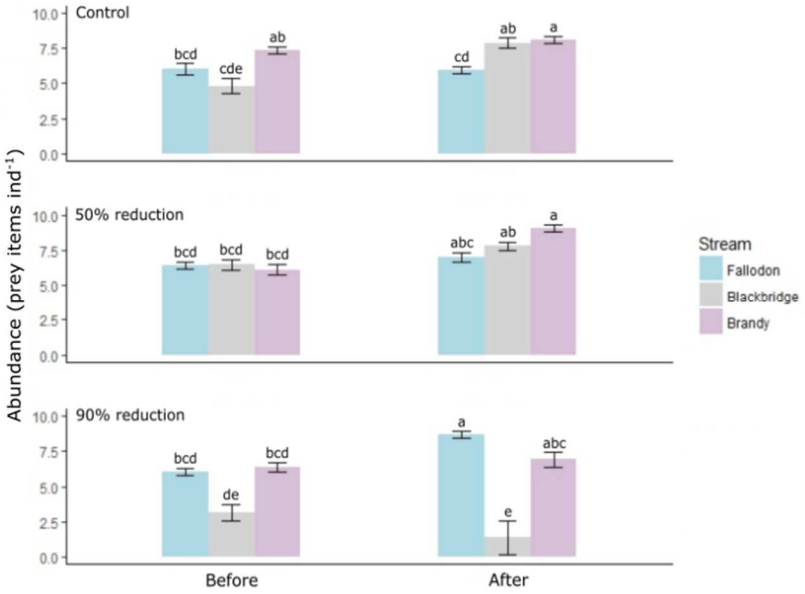

Figure A2.4: Influence of stream and experimental discharge reduction on mean (± standard error) total abundance of prey in the guts of salmon, showing lasting effects of the three different discharge treatments. Results of Tukey's post hoc comparisons shown where mean values sharing the same letter are not significantly different.

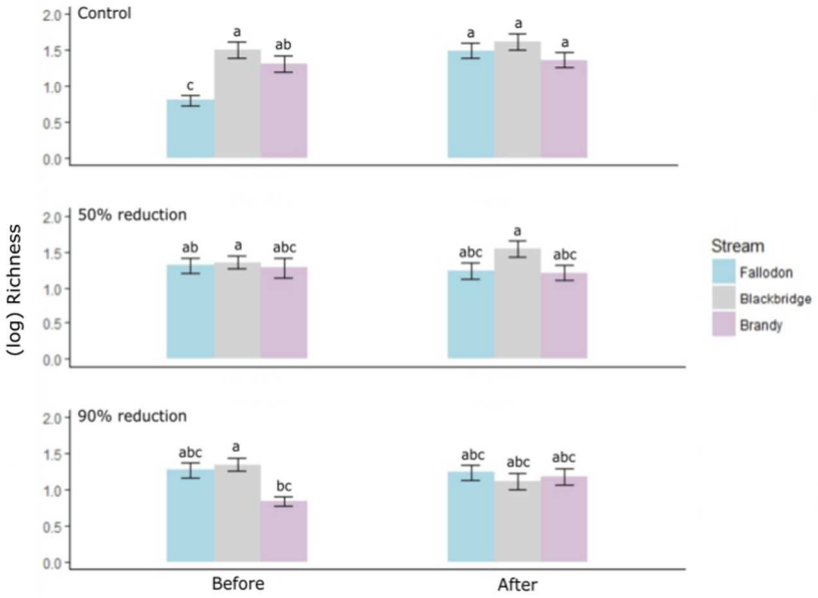

Figure A2.5: Influence of stream and experimental discharge reduction on mean (± standard error) richness of prey in the guts of 0+ trout, showing lasting effects of the three different discharge treatments. Results of Tukey's post hoc comparisons shown where mean values sharing the same letter are not significantly different.

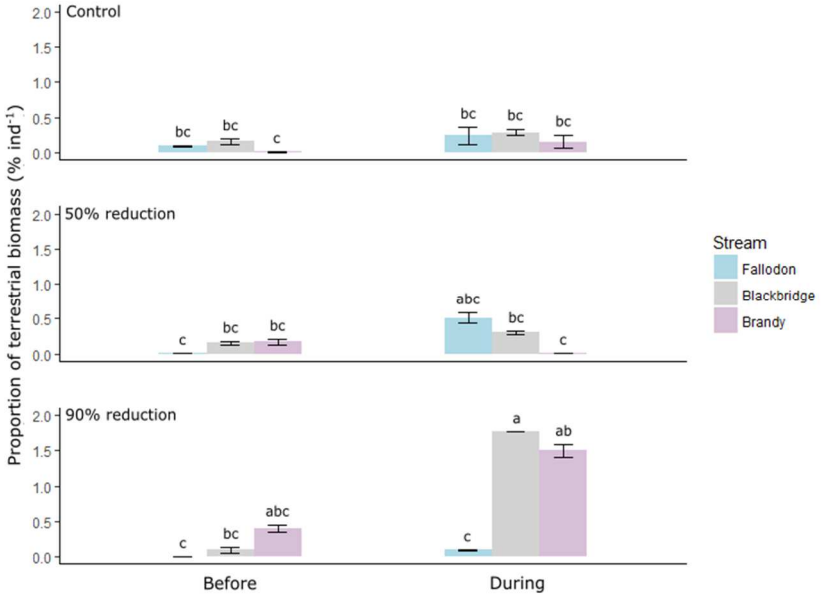

Figure A2.6: Influence of stream and experimental discharge reduction on mean (± standard error) proportion of terrestrial biomass (arc sin transformed) in the guts of ≥2+ trout. Results of Tukey's post hoc comparisons shown, where mean values sharing the same letter are not significantly different.

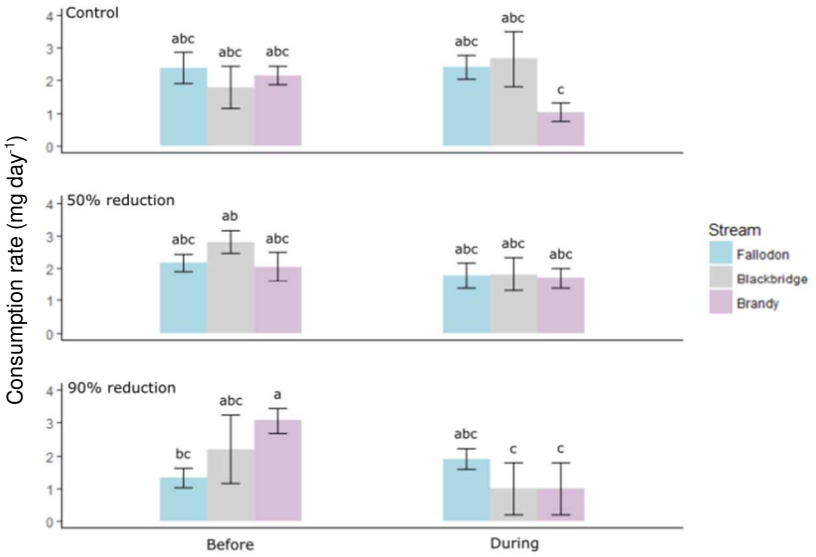

Figure A2.7: Influence of stream and experimental discharge reduction on mean (± standard error) consumption rate (mg day^{-1}) of salmon. Results of Tukey's post hoc comparisons shown where mean values sharing the same letter are not significantly different.

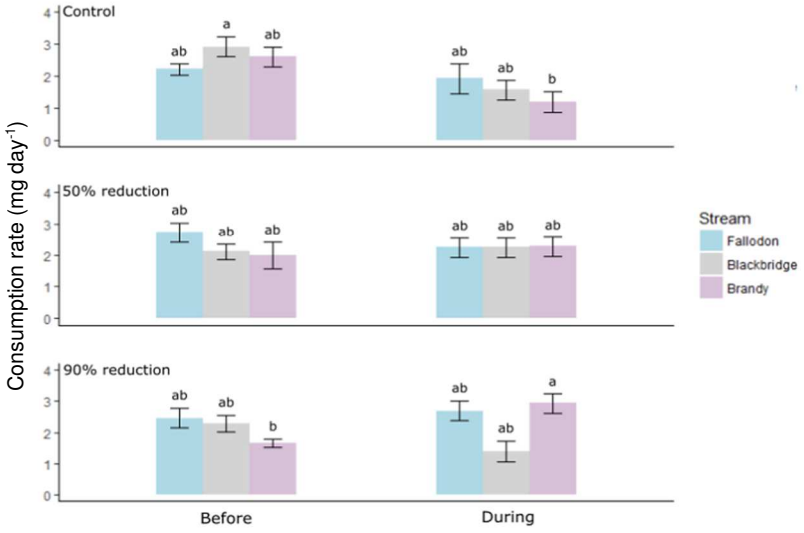

Figure A2.8: Influence of stream and experimental discharge reduction on mean (± standard error) consumption rate (mg day^{-1}) of 0+ trout. Results of Tukey's post hoc comparisons shown where mean values sharing the same letter are not significantly different.

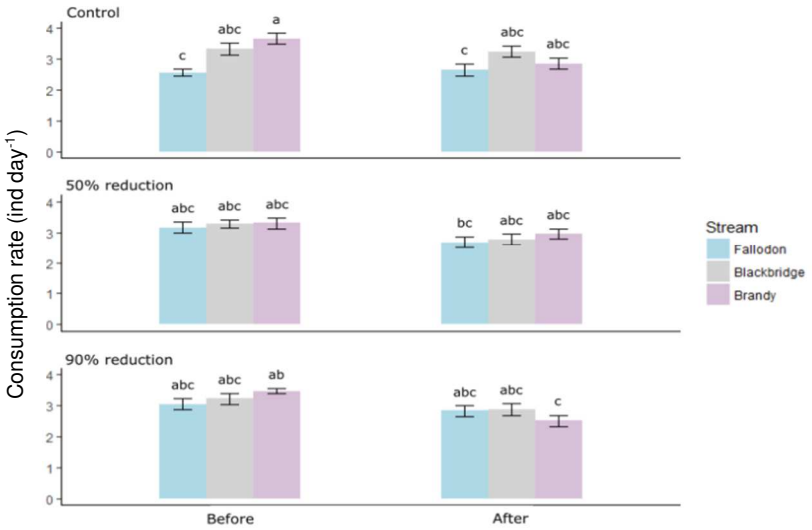

Figure A2.9: Influence of stream and experimental discharge reduction on mean (± standard error) consumption rate (ind day^{-1}) of 1+ trout, showing lasting effects of the three different discharge treatments. Results of Tukey's post hoc comparisons shown where mean values sharing the same letter are not significantly different.

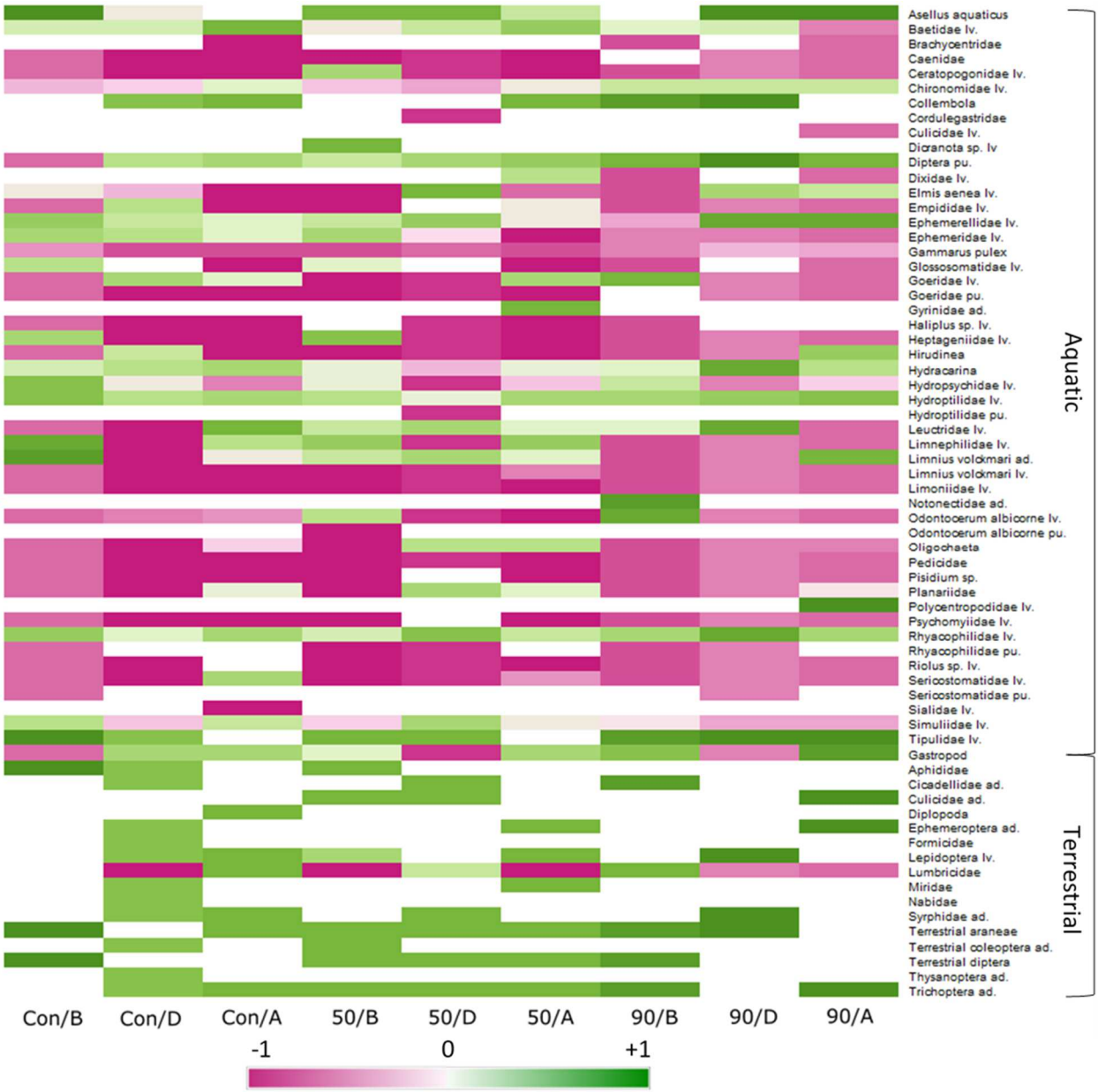

Figure A2.10: Heat map of prey electivity by salmon compared with benthos availability. Dark pink = prey avoidance, light pink/green = prey generally taken in proportion to the relative abundance within the benthos, dark green = prey preference. Gastropods include both terrestrial and aquatic. White gaps are where prey items were not captured within the environment or guts on that specific occasion.

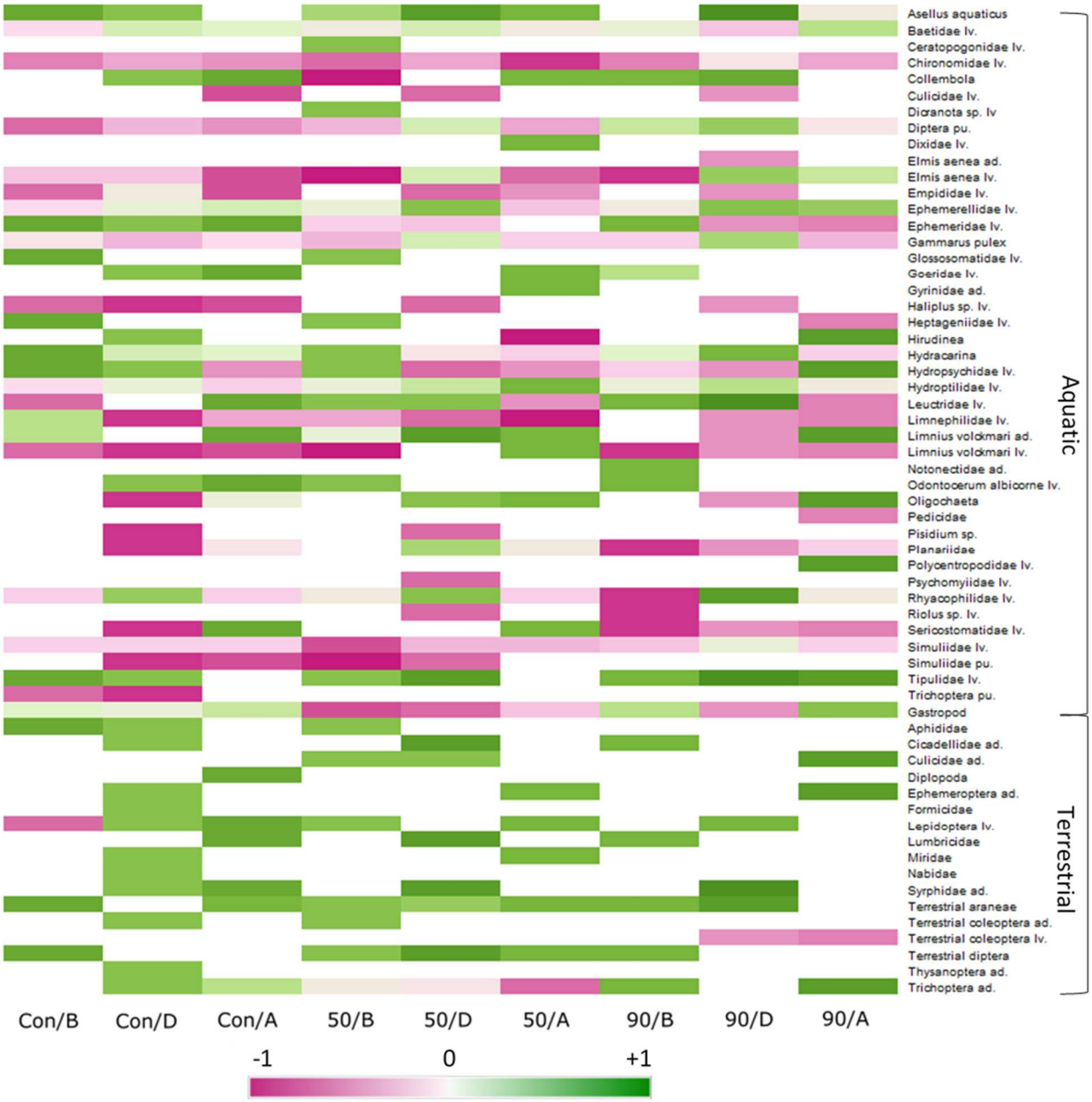

Figure A2.11: Heat map of prey electivity by salmon compared with drift availability. Dark pink = prey avoidance, light pink/green = prey generally taken in proportion to the relative abundance within drift, dark green = prey preference. Gastropods include both terrestrial and aquatic. White gaps are where prey items were not captured within the environment or guts on that specific occasion.

Figure A2.12: Heat map of prey electivity by 0+ trout compared with benthos availability. Dark pink = prey avoidance, light pink/green = prey generally taken in proportion to the relative abundance within the benthos, dark green = prey preference. Gastropods include both terrestrial and aquatic. No colour indicates where prey items were not captured within the environment or guts on that specific occasion.

Figure A2.13: Heat map of prey electivity by 0+ trout compared with drift availability. Dark pink = prey avoidance, light pink/green = prey generally taken in proportion to the relative abundance within the drift, dark green = prey preference. Gastropods include both terrestrial and aquatic. No colour indicates where prey items were not captured within the environment or guts on that specific occasion.

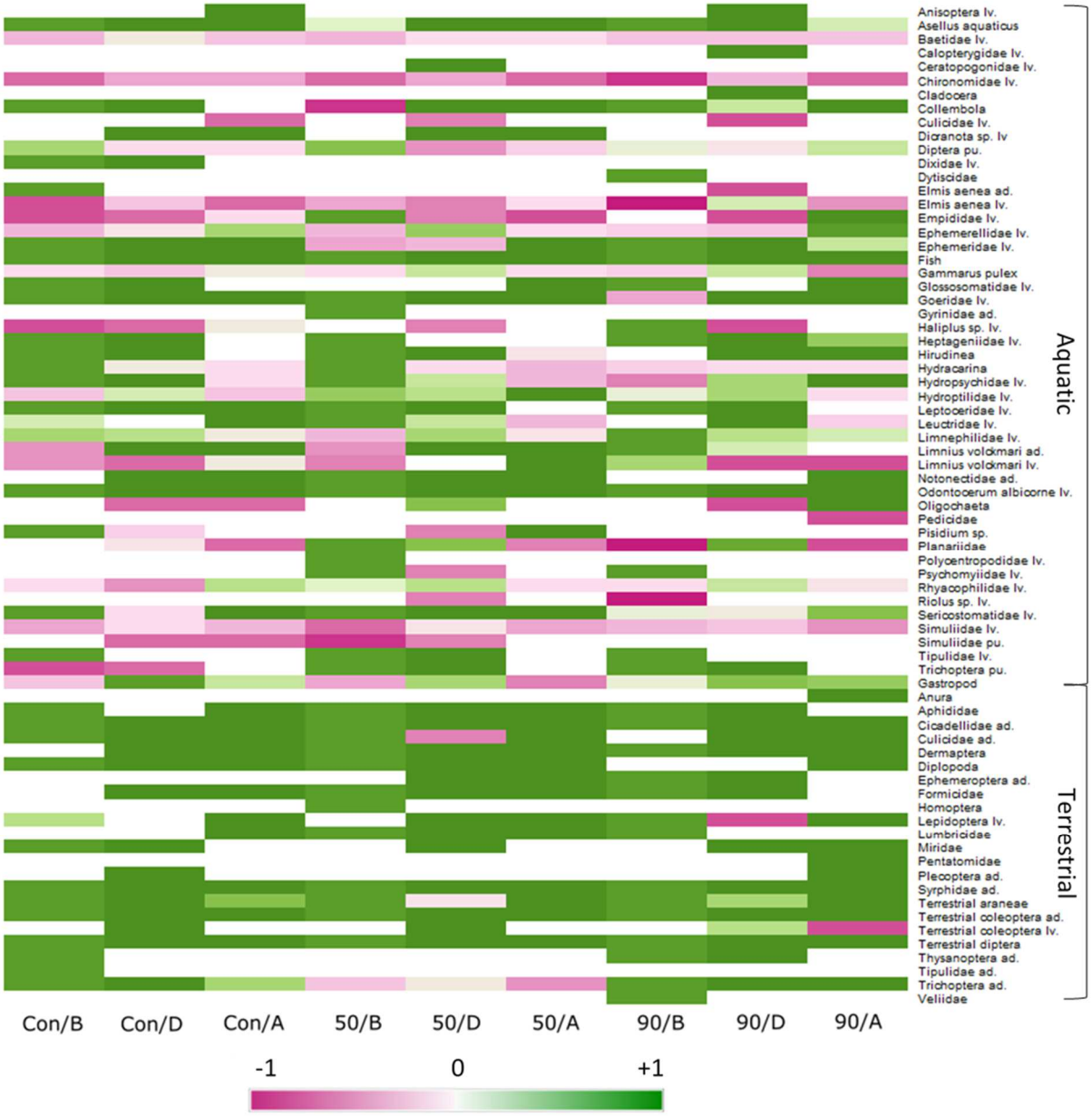

Figure A2.14: Heat map of prey electivity by 1+ trout compared with drift availability. Dark pink = prey avoidance, light pink/green = prey generally taken in proportion to the relative abundance within the drift, dark green = prey preference. Gastropods include both terrestrial and aquatic. White gaps are where prey items were not captured within the environment or guts on that specific occasion

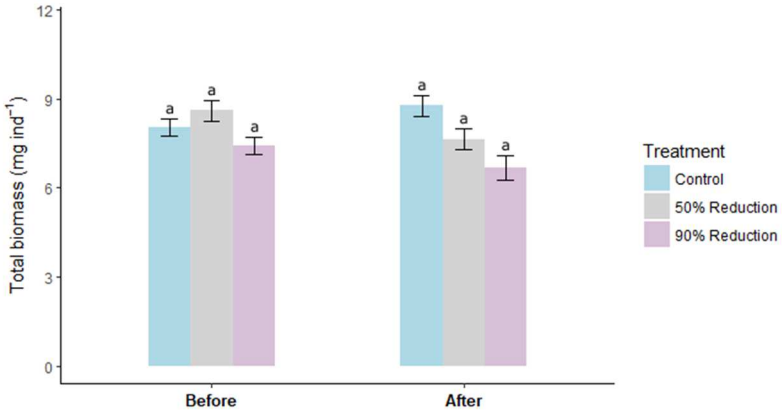

Figure A2.15: Lasting effects of experimental discharge reduction treatments on mean (± standard error) total biomass of prey (mg ind^{-1}) in the guts of ≥2+ trout. Results of Tukey's post hoc comparisons shown: mean values sharing the same letter are not significantly different.

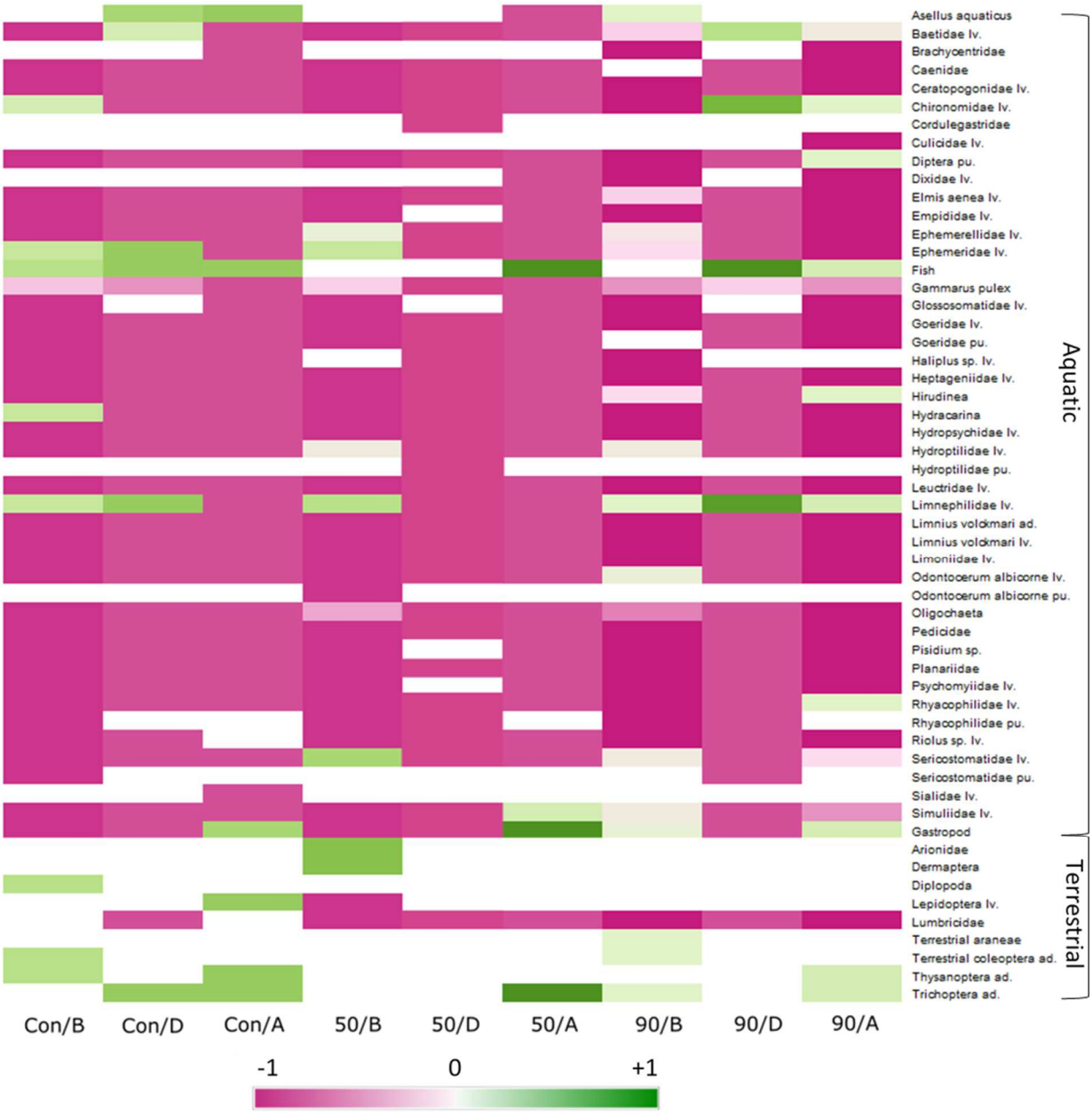

Figure A2.16: Heat map of prey electivity by ≥2+ trout compared with benthos availability. Dark pink = prey avoidance, light pink/green = prey generally taken in proportion to the relative abundance within the benthos, dark green = prey preference. Gastropods include both terrestrial and aquatic. White gaps are where prey items were not captured within the environment or guts on that specific occasion.

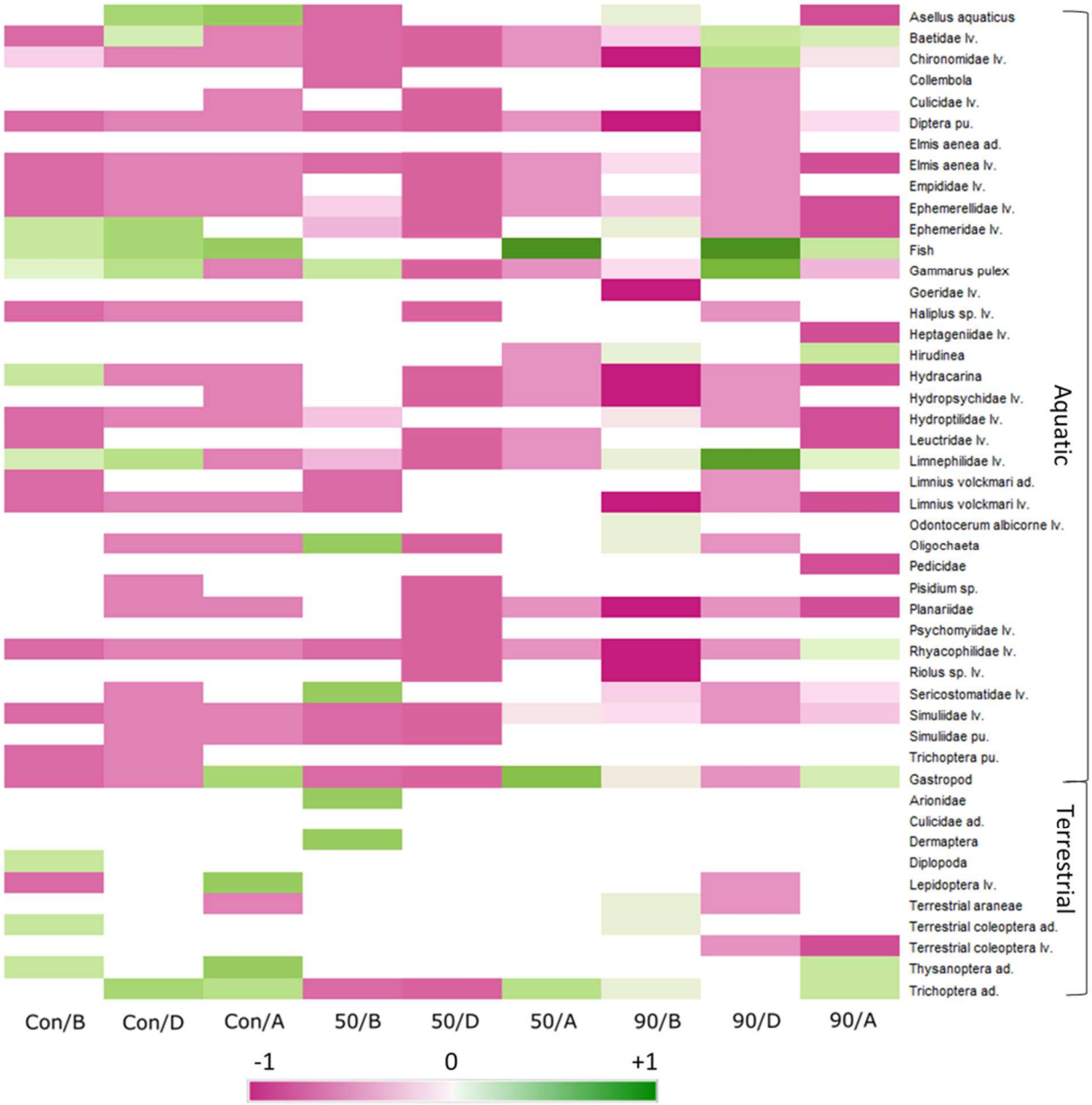

Figure A2.17: Heat map of prey electivity by ≥2+ trout compared with drift availability. Dark pink = prey avoidance, light pink/green = prey generally taken in proportion to the relative abundance within the drift, dark green = prey preference. Gastropods include both terrestrial and aquatic. White gaps are where prey items were not captured within the environment or guts on that specific occasion.

Appendix 3

Table A3.1: Start date, day/month, and (number of days) for each MPD detection period split and end of experiment date in each Year and Stream. Note: number of days rounded to the nearest whole day for clarity.

			Pre-manipulation flow	Treatment flow		Post gut flushing	Return to normal flow	Experiment end
Year	**Stream**	**Treatment**	**Before**	**During 1**	**During 2**		**After**	
2015	Fallodon	Control	11/08 (5 hours)	12/08 (9)	21/08 (9)	03/09 (2)	06/09 (9)	15/09
	Blackbridge	50% reduction	02/08 (9)	12/08 (9)	21/08 (9)	03/09 (2)	06/09 (9)	15/09
	Brandy	90% reduction	01/08 (9)	11/08 (9)	20/08 (9)	02/09 (2)	05/09 (9)	14/09
2016	Fallodon	90% reduction	31/07 (9)	09/08 (9)	19/08 (9)	31/08 (2)	03/09 (9)	12/09
	Blackbridge	Control	31/07 (9)	10/08 (9)	19/08 (9)	01/09 (2)	04/09 (9)	13/09
	Brandy	50% reduction	31/07 (9)	10/08 (9)	19/08 (9)	01/09 (2)	04/09 (9)	13/09
2017	Fallodon	50% reduction	29/07 (9)	08/08 (9)	17/08 (9)	30/08 (2)	02/09 (9)	11/09
	Blackbridge	90% reduction	31/07 (9)	10/08 (9)	19/08 (9)	01/09 (2)	04/09 (9)	13/09
	Brandy	Control	31/07 (9)	09/08 (9)	18/08 (9)	31/08 (2)	03/09 (9)	12/09

Table A3.2: Number of salmonids and (detections) after each data preparation step

Data preparation step	Salmon	Trout
Initial numbers	39 (1,023,586)	427 (3,254,280)
1)	36 (985,999)	416 (3,167,754)
2)	34 (985,993)	409 (3,167,287)
3)	33 (828,695)	382 (2,696,266)
4)	33 (828,695)	382 (2,693,828)
5)	29 (828,690)	337 (2,693,783)

Table A3.3: Number of individual fish that were detected by the MPD on the array and successfully logged for each species and cohort by discharge treatment and detection period during the day and at night.

Treatment	Detection period	Species	Age	Day		Night	
				Number of fish	Number of detections	Number of fish	Number of detections
Control	Before	Salmon		7	152,186	6	8,674
		Trout	0+	15	30,775	15	35,317
			1+	25	8,371	22	5,817
			≥2+	10	10,494	12	9,036
	During 1	Salmon		11	107,941	8	1,8251
		Trout	0+	19	62,863	20	137,614
			1+	25	104,144	26	11,874
			≥2+	12	1922	15	1,045
	During 2	Salmon		10	66,468	5	4226
		Trout	0+	22	132,109	17	110,663
			1+	26	106,095	25	25,225
			≥2+	6	316	11	179
	After	Salmon		6	23,788	6	24,575
		Trout	0+	22	66,825	21	69,155
			1+	19	2,868	20	3,389
			≥2+	6	27	8	1,506
50% reduction	Before	Salmon		2	5,184	2	5,545
		Trout	0+	37	62,191	35	18,033
			1+	28	32,724	32	6,834
			≥2+	6	695	6	2,192
	During 1	Salmon		2	3,460	2	2,820
		Trout	0+	43	53,495	43	37,910
			1+	30	43,822	29	70,666
			≥2+	5	164	6	69
	During 2	Salmon		3	1,453	3	717
		Trout	0+	34	22,867	46	60,664
			1+	23	11,496	25	7,083
			≥2+	2	129	3	54
	After	Salmon		2	11	2	17
		Trout	0+	31	51,550	37	27,417
			1+	14	9,687	18	8,944
			≥2+	1	1	4	296
90% reduction	Before	Salmon		6	4,537	6	33,488
		Trout	0+	24	44,081	27	12,834
			1+	22	15,637	24	25,369
			≥2+	8	8,111	9	1,293
	During1	Salmon		6	31,473	7	14,207
		Trout	0+	33	65,805	40	37,767
			1+	26	74,536	38	23,844
			≥2+	3	1,153	6	1,976
	During2	Salmon		4	521	3	113
		Trout	0+	26	211,783	43	164,793
			1+	10	23,777	20	27,628
			≥2+	3	19	13	506
	After	Salmon		7	153,203	4	125,042
		Trout	0+	28	251,095	31	186,082
			1+	16	25,279	18	13,315
			≥2+	5	3,606	6	7,182

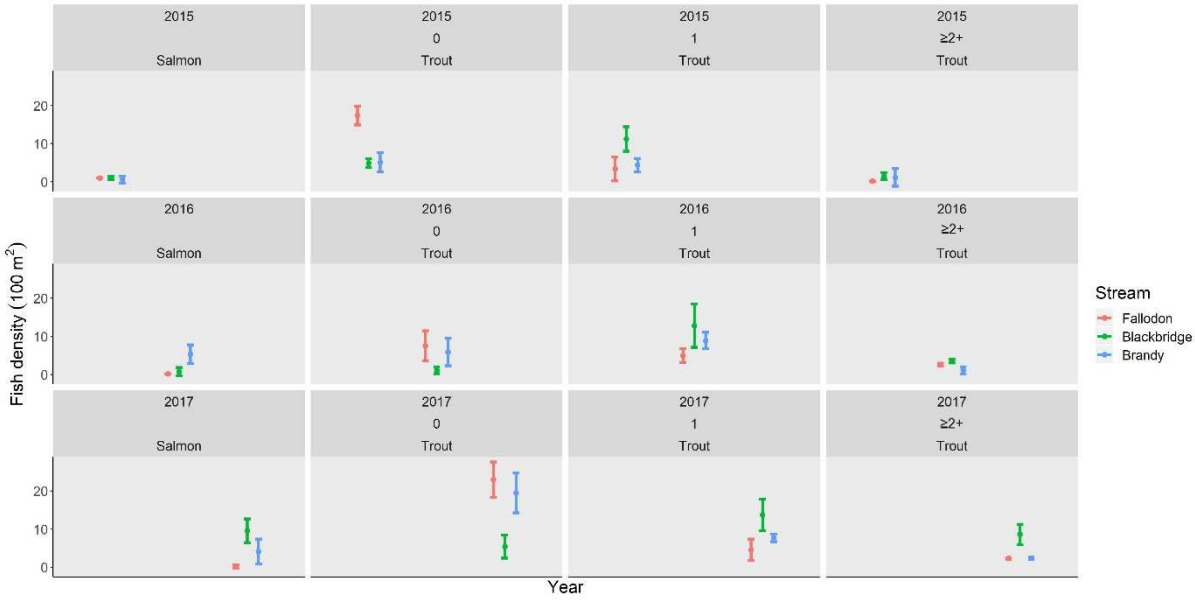

Figure A3.1: Fish density (100m^2) in the Before occasion for each year and stream combination of species and cohort.

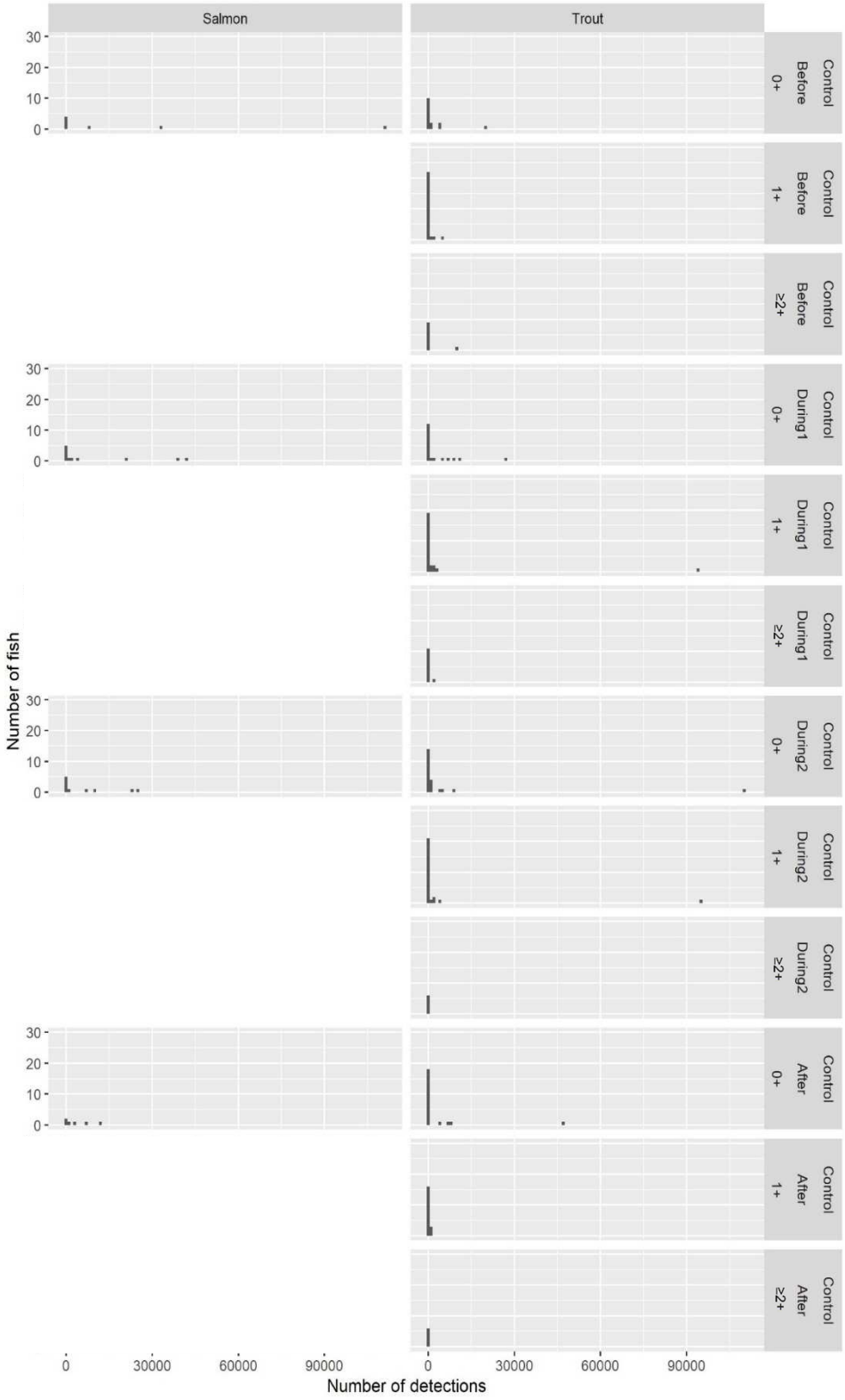

Figure A3.2: Number of detections contributed by each fish in the control treatment in the day.

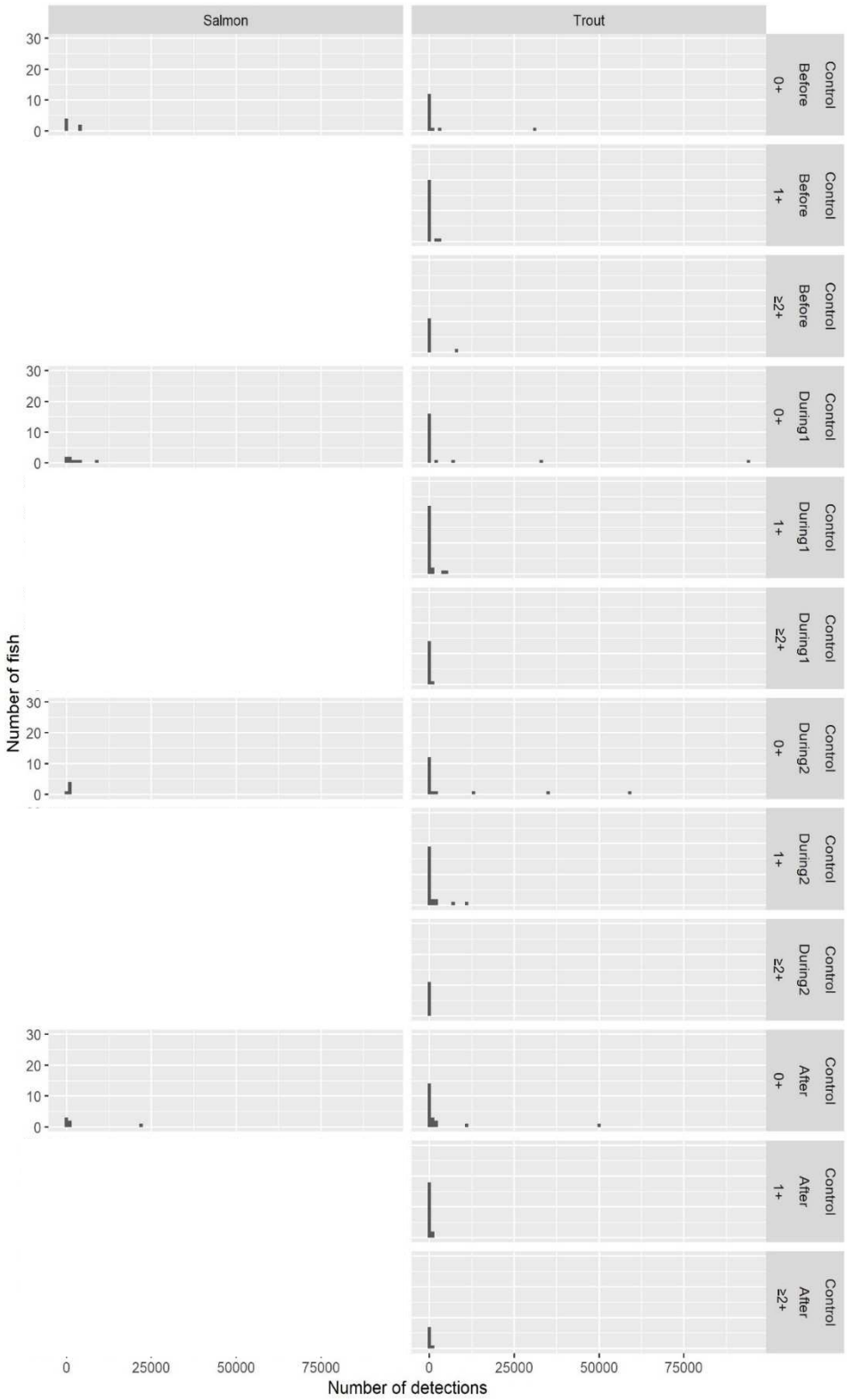

Figure A3.3: Number of detections contributed by each fish in the control treatment at night.

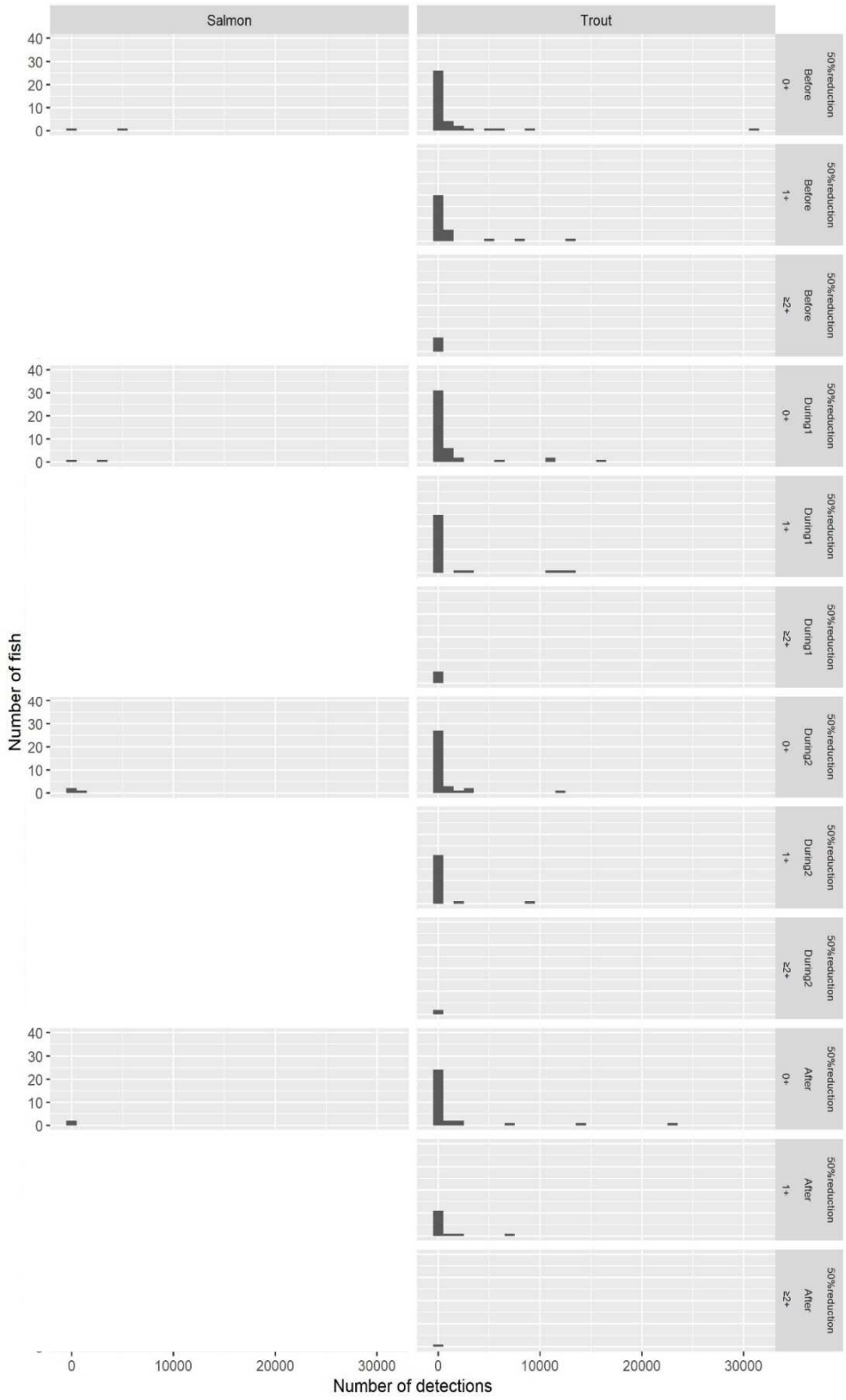

Figure A3.4: Number of detections contributed by each fish in the 50% reduction treatment in the day.

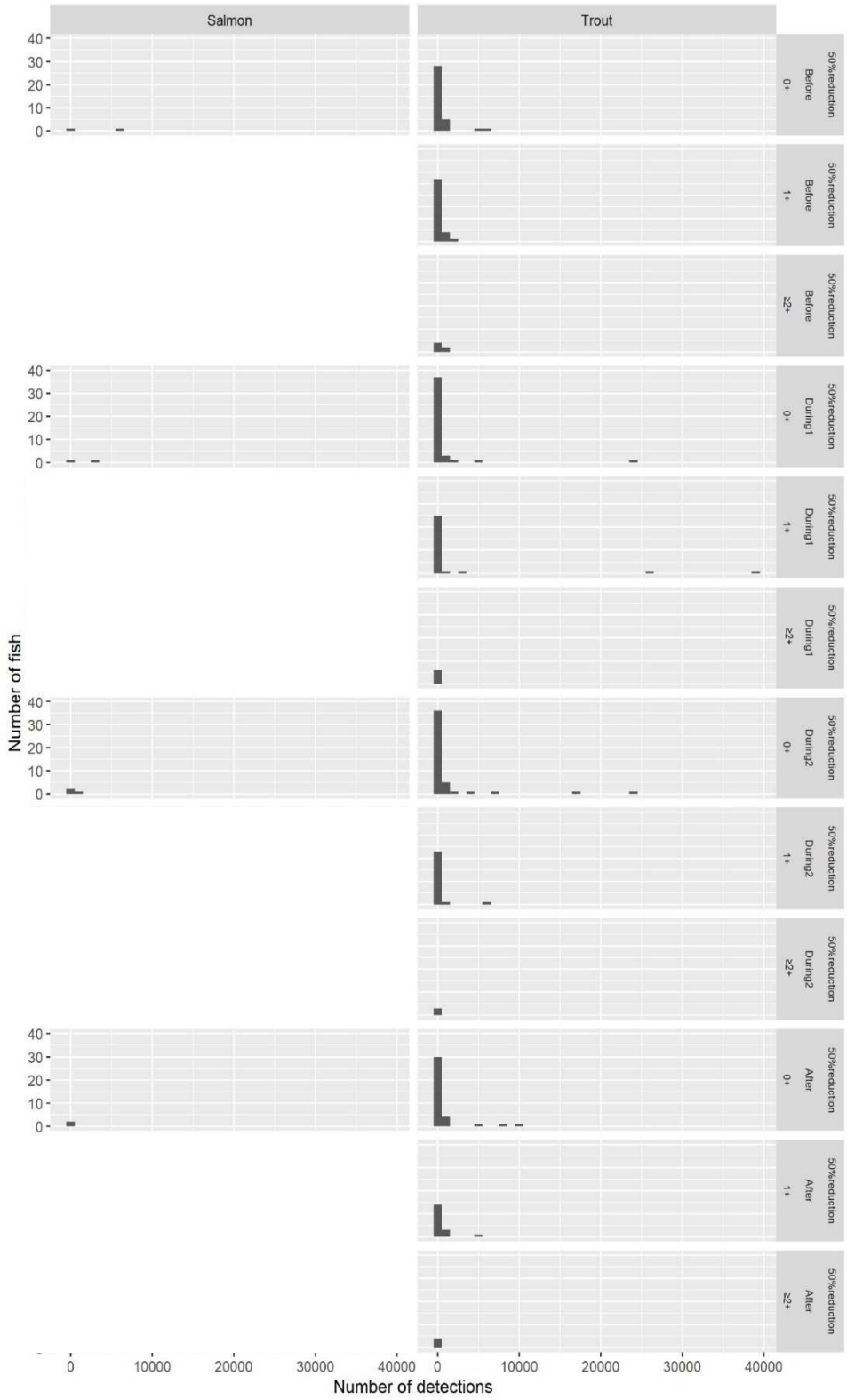

Figure A3.5: Number of detections contributed by each fish in the 50% reduction treatment at night.

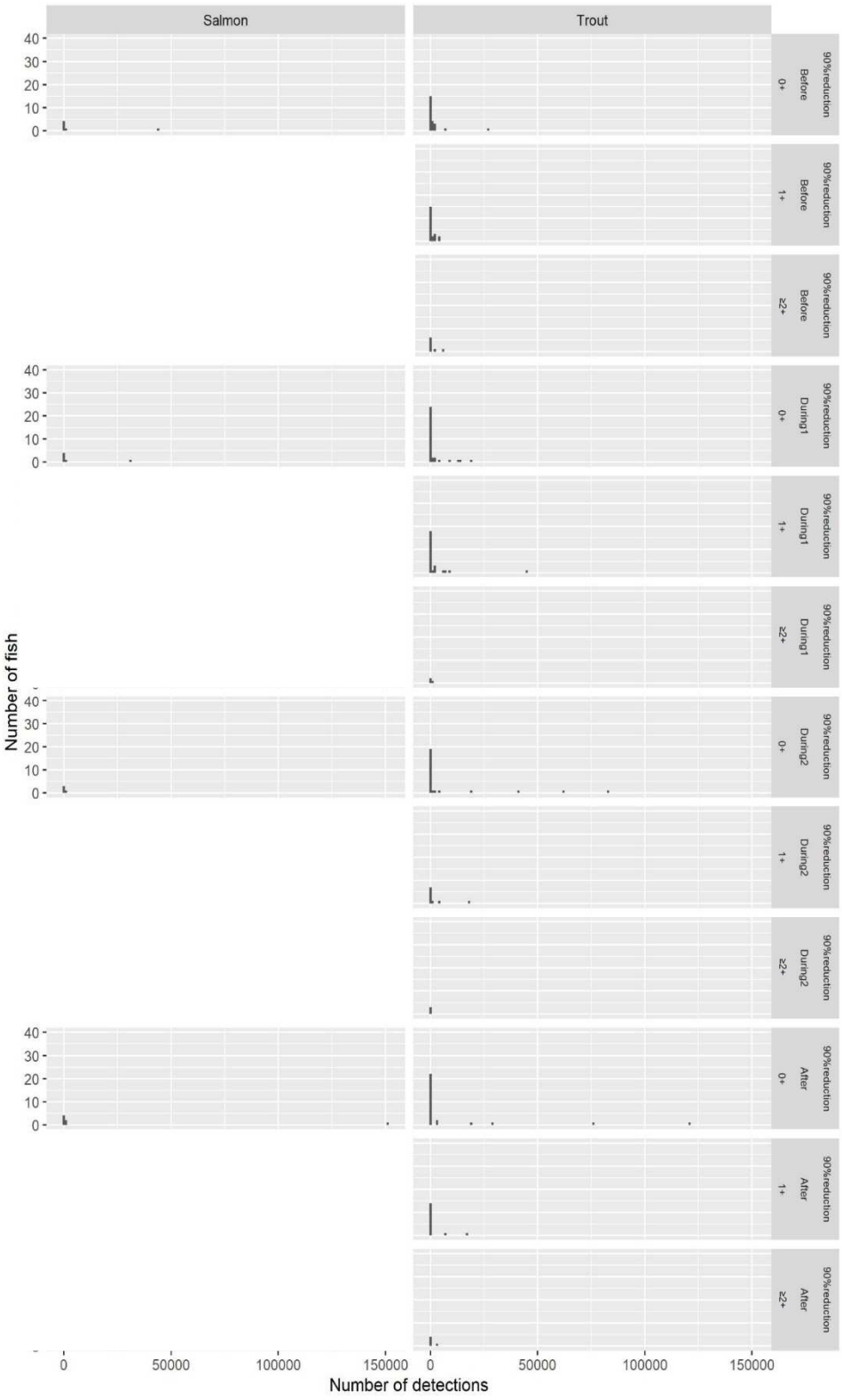

Figure A3.6: Number of detections contributed by each fish in the 90% reduction treatment in the day.

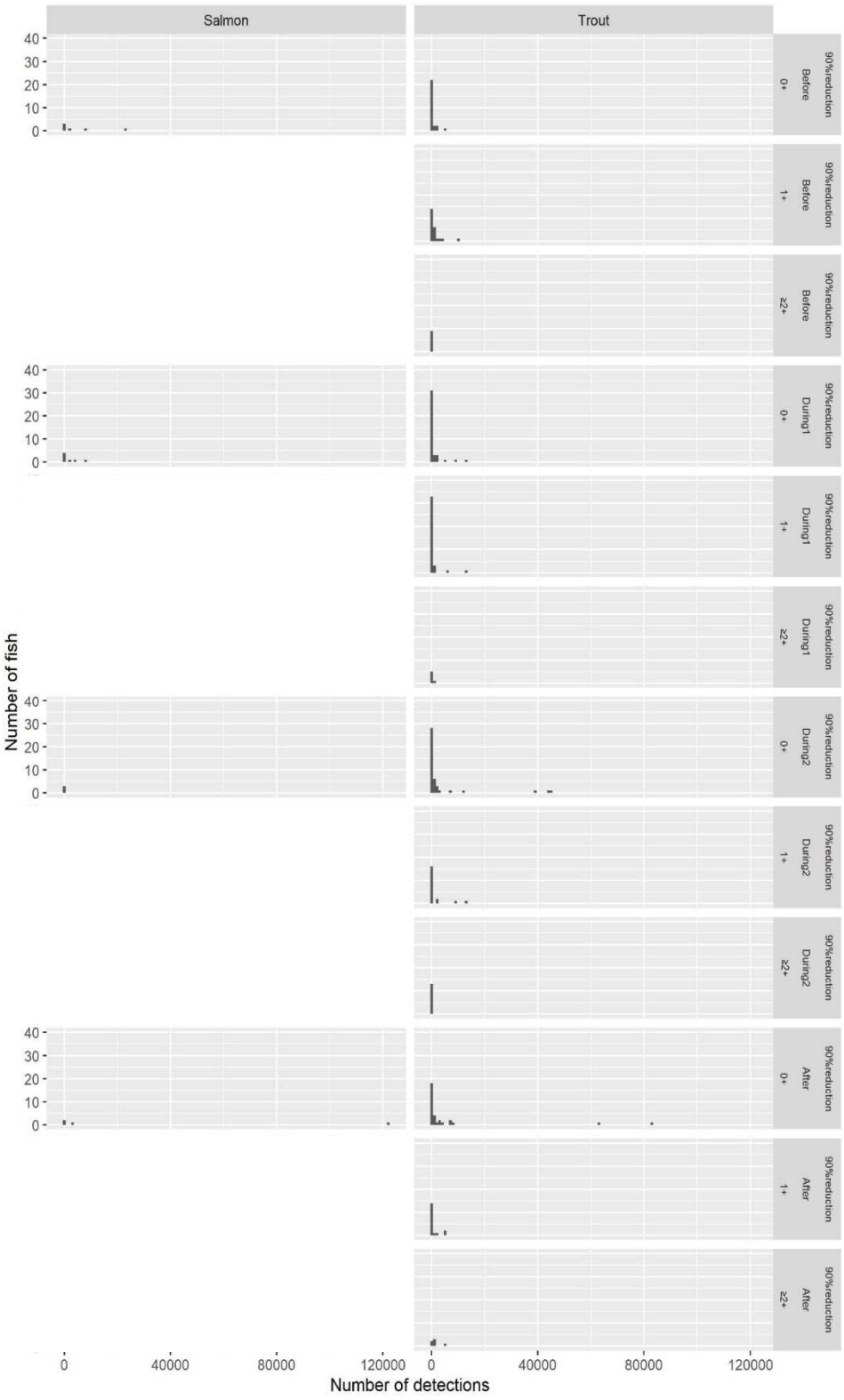

Figure A3.7: Number of detections contributed by each fish in the 90% reduction treatment at night.

Appendix 4

Table A4.1: Total number of salmonids caught within each experimental discharge treatment per stream and occasion.

		Salmon	0+ trout	1+ trout	≥2+ trout
Control					
	Fallodon				
	Before	9	69	52	15
	During	16	43	18	4
	After	18	101	42	2
	Blackbridge				
	Before	4	87	58	32
	During	4	92	36	22
	After	9	188	62	38
	Brandy				
	Before	143	91	201	123
	During	34	64	103	51
	After	123	162	223	101
50% reduction					
	Fallodon				
	Before	50	239	99	31
	During	13	97	32	9
	After	30	171	57	42
	Blackbridge				
	Before	14	194	36	2
	During	9	161	18	1
	After	21	306	35	2
	Brandy				
	Before	12	20	170	54
	During	29	71	110	23
	After	45	114	206	53
90% reduction					
	Fallodon				
	Before	66	71	114	14
	During	36	68	56	3
	After	47	118	85	4
	Blackbridge				
	Before	2	194	36	2
	During	9	161	18	1
	After	21	306	35	2
	Brandy				
	Before	16	69	159	29
	During	4	58	69	8
	After	10	141	155	16

Table A4.2: Total number of tagged individuals that were caught in all three occasions within one experimental year in each discharge treatment.

	Salmon	0+ trout	1+ trout	≥2+ trout
Treatment				
Control	17	28	86	73
50% reduction	13	50	96	24
90% reduction	6	27	76	18

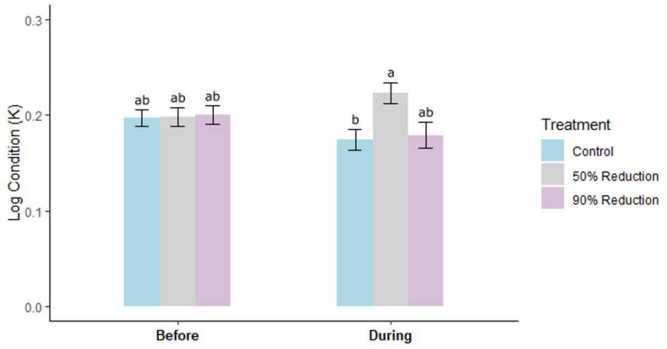

Figure A4.1: Influence of experimental discharge reduction treatments on mean (±standard error) (log) condition (K) of salmon. Results of Tukey's post hoc comparisons shown: mean values sharing the same letter are not significantly different.

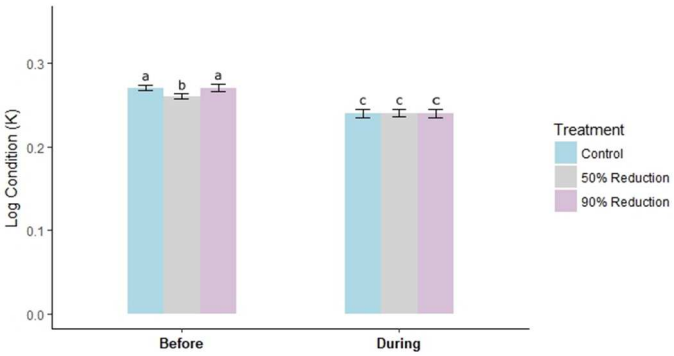

Figure A4.2: Influence of experimental discharge reduction treatments on mean (±standard error) (log) condition (K) of 0+ trout. Results of Tukey's post hoc comparisons shown: mean values sharing the same letter are not significantly different.

Table A4.3: Density per 100 m^2 (± se) of salmonids Before and After the experimental discharge reduction treatments per stream. Grey boxes indicate reduction in density between the Before and After occasions.

			Salmon	0+ trout	1+ trout	≥2+ trout
Control						
	Fallodon					
		Before	0.64 (0.9)	5.08 (2.5)	4.36 (1.8)	1.14 (1.3)
		After	1.42 (1.5)	7.98 (2.04)	3.38 (2.50)	0.15 (1.03)
	Blackbridge					
		Before	0.16 (0.01)	7.57 (3.9)	4.96 (1.8)	2.61 (0.4)
		After	0.44 (0.38)	17.36 (3.05)	5.63 (1.1)	0.44 (0.38)
	Brandy					
		Before	10.31 (4.1)	5.39 (3)	13.72 (4.2)	8.61 (2.7)
		After	8.03 (10.83)	10.50 (7.03)	14.81 (4.74)	6.61 (0.95)
50% reduction						
	Fallodon					
		Before	4.11 (3.8)	19.53 (5.2)	7.70 (1)	2.41 (0.3)
		After	2.34 (1)	13.76 (3.41)	5.66 (1.96)	3.45 (2.51)
	Blackbridge					
		Before	0.89 (0.6)	17.38 (2.5)	3.37 (3.1)	0.17 (0.01)
		After	2.31 (1.58)	27.23 (2.82)	2.64 (0.29)	0.18 (0.01)
	Brandy					
		Before	0.72 (1.1)	1.12 (0.9)	12.82 (5.7)	3.58 (0.5)
		After	2.01 (1.59)	7.37 (3.91)	12.86 (2.73)	3.41 (0.7)
90% reduction						
	Fallodon					
		Before	5.34 (2.5)	5.88 (3.6)	8.91 (2.2)	1.08 (1)
		After	3.62 (0.88)	9.26 (2.88)	6.48 (7.03)	0.31 (0.68)
	Blackbridge					
		Before	0.17 (0.4)	23.01 (4.6)	4.60 (2.8)	2.30 (0.2)
		After	0.21 (0.73)	16.32 (3.48)	3.72 (0.89)	1.33 (1.19)
	Brandy					
		Before	1.05 (0.4)	4.87 (1.1)	11.22 (3.2)	1.53 (0.9)
		After	0.49 (0.36)	8.51 (4.43)	9.77 (0.67)	0.84 (0.11)

Table A4.4: Results of ANOVA testing for experimental effects on PIT tagged salmonid growth rates (% g g^{-1} DD^{-1}) that were caught on all three sampling occasions.

	Growth rate				
Source	**df**	**ss**	**ms**	**F**	***p***
Salmon					
Year	1	.00005	.00005	6.44	*
Treatment	1	.00016	.00016	18.93	***
Occasion	1	.00004	.00004	.04	
Treatment:Occasion	2	.00001	.00005	.66	
Residuals	16	.00014	.00008		
0+ trout					
Year	2	.00017	.00005	3.53	*
Treatment	2	.00001	.00006	.04	
Occasion	1	.00003	.00003	2.52	
Treatment:Occasion	2	.00004	.00002	.01	
Residuals	206	.00311	.00001		
1+ trout					
Year	2	.00002	.00001	.44	
Treatment	2	.00003	.00001	.51	
Occasion	1	.00009	.00009	.31	
Treatment:Occasion	2	.00011	.00005	1.9	
Residuals	548	1.692	.003		
≥2+ trout					
Year	2	.00001	.00007	.39	
Treatment	2	.00003	.00001	.08	
Occasion	1	.00005	.00005	.26	
Treatment:Occasion	2	.00002	.00001	.54	
Residuals	264	5.05	.00019		

****p <0.001, **p <0.01, *p <0.05*, Blanks = *p >0.05*.

Table A4.5: Results of ANOVA testing for stream specific experimental effects on PIT tagged salmonid growth rates (% g g^{-1} DD^{-1}) that were caught on all three sampling occasions.

	Growth rate				
Source	**df**	**ss**	**ms**	**F**	***P***
Salmon					
Year	1	.00005	.00005	6.44	*
Treatment	1	.00016	.00016	18.93	***
Occasion	1	.00004	.00004	.04	
Stream	1	.00002	.00002	.03	
Treatment:Occasion:Stream	2	.00001	.00005	.66	
Residuals	15	.014	.00008		
0+ trout					
Year	2	.00010	.00005	3.88	*
Treatment	2	.00001	.00006	.04	
Occasion	1	.00003	.00003	2.77	
Stream	2	.00023	.00011	8.36	***
Treatment:Occasion:Stream	11	.00019	.00001	1.31	
Residuals	195	.268	.001		
1+ trout					
Year	2	.00002	.00001	.43	
Treatment	2	.00003	.00001	.50	
Occasion	1	.00009	.00009	.31	
Stream	2	.00002	.00001	.03	
Treatment:Occasion:Stream	11	.00029	.00002	.85	
Residuals	537	1.675	.003		
≥2+ trout					
Year	2	.00001	.00007	.38	
Treatment	2	.00003	.00001	.07	
Occasion	1	.00005	.00005	.25	
Stream	2	.00003	.00001	.08	
Treatment:Occasion:Stream	10	.00002	.00002	.12	
Residuals	254	5.05	.019		

****p <0.001, **p <0.01, *p <0.05*, Blanks = *p >0.05*.

Table A4.6: Results of ANOVA testing lasting stream effects of reduced discharge on mean length (cm), mass (g) and condition (K) of salmonids.

	Length (cm)					Mass (g)					Condition (K)				
Source	**df**	**ss**	**ms**	**F**	***p***	**df**	**ss**	**ms**	**F**	***P***	**df**	**ss**	**ms**	**F**	***p***
Salmon															
Year	2	16.76	8.38	173.46	***	2	152.75	76.37	162.16	***	2	.22	.11	16.91	***
Treatment	2	.84	.42	8.77	***	2	8.18	4.09	8.68	***	2	.02	.01	2.50	
Occasion	1	2.06	2.06	42.79	***	1	15.43	15.43	32.76	***	1	.14	.14	21.51	***
Stream	2	.03	.01	.33		2	.27	.13	.29		2	.01	.01	.54	
Treatment:Occasion:Stream	11	2.42	.22	4.57	***	11	23.59	2.14	4.55	***	11	.24	.02	3.31	***
Residuals	609	29.42	.04			609	286.82	.47			609	4.07	.01		
0+ trout															
Year	2	.30	.30	12.27	***	2	.19	.19	.84		2	1.45	1.54	191.32	***
Treatment	2	.69	.34	13.96	***	2	5.42	2.71	11.95	***	2	.06	.03	4.31	*
Occasion	1	21.05	21.04	852.81	***	1	151.49	151.49	667.55	***	1	2.14	2.14	282.93	***
Stream	2	2.63	1.31	53.36	***	2	25.99	12.99	57.27	***	2	.05	.03	3.81	*
Treatment:Occasion:Stream	12	1.07	.08	3.62	***	12	10.84	.90	3.98	***	12	.41	.03	4.59	***
Residuals	2801	69.15	.02			2801	635.88	.22			2801	21.26	.007		
1+ trout															
Year	2	3.12	1.56	120.66	***	2	26.11	13.05	105.75	***	2	.45	.22	6.40	**
Treatment	2	.16	.08	6.26	**	2	1.90	.95	7.69	***	2	.11	.05	1.51	
Occasion	1	1.49	1.49	115.48	***	1	5.35	5.63	45.64	***	1	1.41	1.41	39.43	***
Stream	2	1.65	.82	64.14	***	2	17.28	8.64	69.99	***	2	.05	.03	.69	
Treatment:Occasion:Stream	12	.86	.07	5.57	***	12	7.85	.65	5.30	***	12	.45	.04	1.04	
Residuals	1868	24.16	.01			1868	230.6	.12			1868	66.97	.04		
≥2+ trout															
Year	2	1.05	1.05	42.10	***	2	14.10	14.09	56.23	***	2	.43	.44	5.87	*
Treatment	2	.51	.26	10.25	***	2	5.26	2.63	10.48	***	2	.18	.09	1.24	
Occasion	1	.02	.02	.85		1	.002	.001	.006		1	.16	.16	2.19	
Stream	2	6.00	3.00	119.89	***	2	49.49	24.75	98.73	***	2	.17	.08	1.15	
Treatment:Occasion:Stream	12	1.13	.09	3.79	***	12	12.82	1.07	4.27	***	12	1.13	.09	1.27	
Residuals	617	15.47	.02			617	154.90	.25			617	45.84	.07		

****p <0.001, **p <0.01, *p <0.05*, Blanks = *p >0.05*.

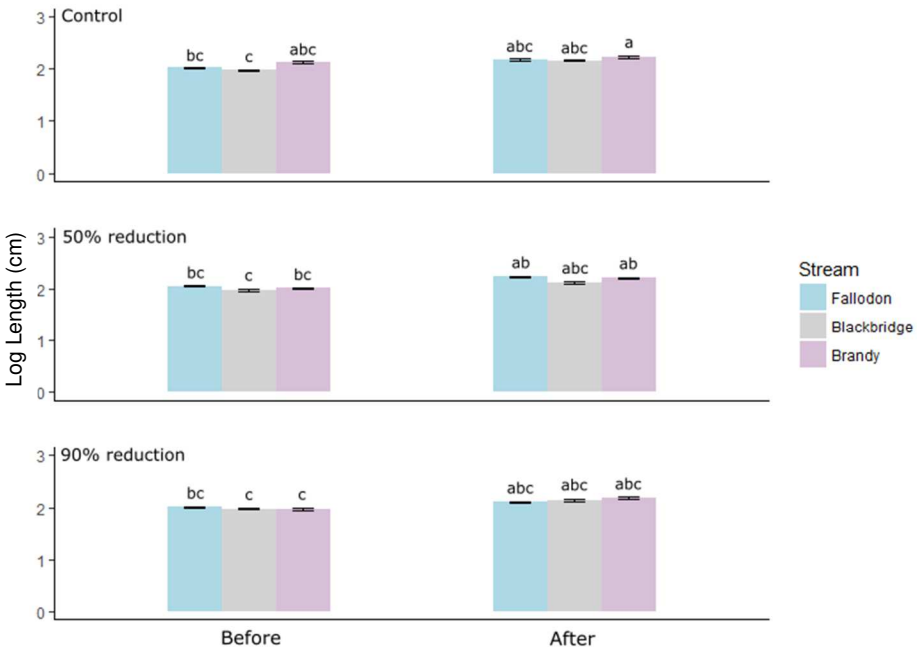

Figure A4.3: Influence of stream and experimental discharge reduction on mean (± standard error) (log) length (cm) of 0+ trout, showing lasting effects of the three different discharge treatments. Results of Tukey's post hoc comparisons shown, where mean values sharing the same letter are not significantly different.